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VOLUME 85, NUMBER 1

NOVEMBER 17, 1941

CONTENTS

- Large Molecules Through Atomic Spectacles. HUGH S. TAYLOR 1
- Crystalline Diphtheria Antitoxin. JOHN H. NORTHROP 13
- The Method of Activation of Melanophores and the Limitations of Melanophore Responses in the Catfish *Ameiurus*. G. H. PARKER 18
- Genetics of *Paramecium bursaria*, II. Self-Differentiation and Self-Fertilization of Clones. H. S. JENNINGS 25
- The "Mule" Pheasant. THOMAS HUME BISSENETTE 49
- Some Pre-Armada Propagandist Poetry in England (1585-1586). TUCKER BROOKE 71
- The Ship of the Soul on a Group of Grave-Stelae from Terenuthis. CAMPBELL BONNER 84

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American Philosophical
Society

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VOLUME 85, NUMBER 2

JANUARY 24, 1942

CONTENTS

Long Enduring Meteor Trains.

CHARLES P. OLIVIER 93

An Analysis of Vertical Oscillations in the Southern North Atlantic.

H. R. SEIWELL 136

Paleocene Faunas of the Polecat Bench Formation, Park County, Wyoming.
Part II, Lizards.

CHARLES W. GILMORE 159

Studies of Living Nerves. VIII, Histories of Nerve Endings in Frog Tadpoles Subjected to Various Injurious Treatments.

CARL CASKEY SPEIDEL 168

New Mutational Segregations from *Oenothera mut. erythrina* De Vries.

GEORGE HARRISON SHULL 183

Montagnais-Naskapi Bands and Family Hunting Districts of the Central and Southeastern Labrador Peninsula.

FRANK G. SPECK AND LOREN C. EISELEY 215

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OF THE
American Philosophical
Society

Held at Philadelphia for Promoting Useful Knowledge

VOLUME 85, NUMBER 3

5052
FEBRUARY 25, 1942

CONTENTS

Electron-Electron Collisions in the Primary Energy Range from 1.3 to 2.6
Million Electron Volts. PAUL E. SHEARIN AND T. EUGENE PARDUE 243

The Microscopy of Mammalian Hair for Anthropologists. F. MARTIN BROWN 250

The Effect of Early and Late Brain Injury upon Test Scores, and the Nature
of Normal Adult Intelligence. D. O. HEBB 275

Sumerian Literature; A Preliminary Survey of the Oldest Literature in the
World. S. N. KRAMER 293

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THE AMERICAN PHILOSOPHICAL SOCIETY
104 SOUTH FIFTH STREET
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Held at Philadelphia for Promoting Useful Knowledge

VOLUME 85, NUMBER 4

JUNE 8, 1942

CONTENTS

- A Quantitative Study of the Productivity of the Foraminifera in the Sea.
EARL H. MYERS 325
- The Health of Registrants and the President's Plan of Rehabilitation.
LEONARD G. ROWNTREE 343
- The Mystery of Cor Caroli.
OTTO STRUVE 349
- A Comparative Study of Grahamellae, Haemobartonellae and Eperythrozoa
in Small Mammals.
ERNEST EDWARD TYZZER 359
- Theoretical Light Curves of Close Eclipsing Systems.
ZDENĚK KOPAL 399
-

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THE AMERICAN PHILOSOPHICAL SOCIETY
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1942

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LARGE MOLECULES THROUGH ATOMIC SPECTACLES

HUGH S. TAYLOR

David B. Jones Professor of Chemistry, Princeton University
(Franklin Medal Lecture, April 24, 1941)

ABSTRACT

The highest resolutions now attainable with the electron microscope permit us to examine objects which are about 40 Ångström units in linear dimension. Interatomic distances are, however, of the order of 1 to 3 Ångström units so that to examine the geometry of the constituent units of molecules it is still necessary to construct and study models made to scale in accordance with the best data of physico-chemical science. The Fisher-Hirschfelder atomic molecules have proved especially useful in this problem of viewing molecules through atomic spectacles. The method of attaching atoms one to another provided by the makers of these models is not very satisfactory. A new method of attachment has been developed which uses the well-known snap-fastener of the rigid head-resilient socket type to produce an attachment which is "positive," or locked against accidental rupture, while permitting full and free rotation between singly bonded atoms. Molecular models so produced have manipulative stability and a flexibility of motion more closely corresponding to the behavior of the molecular structures modelled. In use, these reveal striking results on the folding of polypeptide chains, such as silk and hair and of other fibrous structures. Folding in three dimensions indicates the possibility of many types of orientation of the peptide links with room for large and small side-chains. Models of complex molecules such as the vitamins, sterols, carcinogenic agents, plastics and rubber polymers reveal characteristics of such molecules which are not immediately evident from the older structural formulæ of the chemist.

In the laboratory notebooks of John Dalton in the library of the Manchester Literary and Philosophical Society the earliest efforts to visualize molecules through atomic spectacles were carefully preserved. An entry dated September 6, 1803, gives the following characters of elements

- | | |
|------------|---------------|
| ○ Hydrogen | ● Carbone, |
| ○ Oxygen | pure Charcoal |
| ⊕ Azote | ⊕ Sulphur |

and, a few pages further on, the following examples of Dalton's method of expressing the composition of chemical compounds

- | | |
|---------------------|----------------------|
| ① ○ ① Nitrous Oxide | ○ ○ Water |
| ① ○ Nitrous Gas | ① ○ Ammonia |
| ○ ① ○ Nitric Acid | ○ ● Gaseous Oxide |
| ○ ① ○ Nitrous Acid | of Carbon |
| ① ○ | ○ ● ○ Carbonic Acid |
| ⊕ ○ Sulphurous Acid | ○ ⊕ ○ Sulphuric Acid |

On December 23 last, during a German air-raid on Manchester, the home of one of our sister societies was subjected to wholesale destruction by bomb and incendiary. These historical documents of the beginnings of the modern era in chemistry, the atomic era, may well have fallen victims to "enemy action".

Dalton's symbol for water ○ ○ is significant. In modern dress this would be HO whereas we now write it H₂O. Avogadro had enunciated as early as 1811 the principles that determined which of these alternatives was the correct one but it was not until his fellow-countryman Cannizzaro demonstrated in 1858 the applicability of Avogadro's ideas that general agreement among chemists was reached and the formulæ, which we still use today, were universally accepted. The analytical chemists of the first half of the 19th century provided the quantitative analyses from which the atomic composition of a wide variety of inorganic compounds could be deduced with the aid of the Dalton concept of atoms and atomic weights. With the rise of organic chemistry under Dumas, Liebig, Wohler, Williamson, Frankland and others, organic compounds were first classified in terms of their corresponding types. Thus, hydrocarbons were of the hydrogen type, organic chlorides of the hydrochloric acid type, ethers of the water type and amines of the ammonia type. Gradually the idea of valence in organic chemistry was recognized and carbon shown to be tetravalent as most simply illustrated in methane CH₄. Structural formulæ were developed in which a two-dimensional picture of the component atoms expressed the four valencies of the carbon as typified in such formulæ as propane CH₃·CH₂·CH₃, methyl ether CH₃·O·CH₃, propyl chloride CH₃CH₂CH₂Cl, propyl amine CH₃·CH₂·CH₂·NH₂ and unsaturation was recognized in compounds with double and triple bonds such as ethylene H₂C=CH₂ and acetylene HC≡CH. Later it became clear that molecules having the same atomic content might have different arrangements of atoms, that is to say "isomers" such as CH₃·CH₂·CH₂Cl and CH₃·CHCl·CH₃.

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could exist. Pasteur then recognized that, in the crystals of tartaric acid, there was the phenomenon of left-handed- and right-handedness, that this implied an isomerism in space. van't Hoff and LeBel embodied this concept of stereo-isomerism in the concept of a spatial arrangement of the four valencies of carbon; for example, in methane, the carbon atom was located at the center of a tetrahedron, the hydrogen atoms at the corners of the tetrahedron. Upon that conception of atoms in space the organic chemist worked out by pure processes of reasoning an accurate body of knowledge as to the disposition of atoms in many molecules.

Deductive processes such as these were necessary since the available physical tools were not as yet adequate to the location of atoms in a molecular structure. With a microscope having a good immersion-system it is only possible to resolve details of a size somewhat less than two ten-thousands of a millimeter using ordinary daylight as the light source. An object of such a linear dimension would have as many as a thousand or more atoms side by side in a row. With the invention of the ultramicroscope and using ultraviolet light as the source of illumination, this resolution could be doubled, but, even so, the magnification was still more than 500 times too feeble. The resolution attainable with the electron microscope, the newest tool in the microscope field, can be pushed to 40 Ångström units (10^{-8} cm.) or to approximately 20 atom diameters. To be able to view the individual atoms it would therefore be necessary to improve the resolution still another twenty-fold.

X-RAY ANALYSIS OF CRYSTAL STRUCTURE

It was in 1912 that the first development occurred which permitted the physicist and the chemist definitely to locate the position of atoms in crystalline materials. Laue in Germany and the Braggs in England independently employed the X-rays to discover the orderly arrangement of atoms and molecules, various estimates having placed these atoms in crystals at distances of the order of 10^{-8} cm. This was the right distance for the reflection and diffraction of the short wave-length of the X-rays, the atoms serving the same purpose with these rays that gratings, ruled by hand, had served Rowland and others in the resolution of ordinary light waves. These developments served a central purpose; they showed

that X-rays were in reality light of short wave-length but they also permitted scientists to put on their atomic spectacles, see the actual architecture of crystalline materials and learn that the external form of those crystals, their properties of cleavage, indicated an internal structure consisting of regular arrangements in space of ultimate units, the constituent atoms.

Sodium chloride was revealed as a cubical structure with atoms or rather ions of sodium and chlorine occupying alternately positions at the corners of a cubical structure or lattice (Fig. 1).

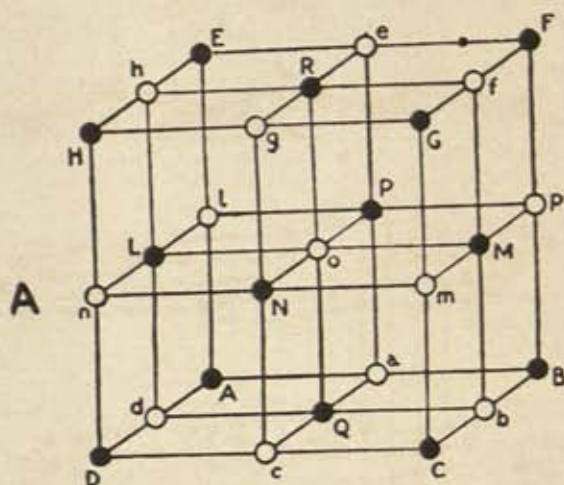


FIG. 1. Cubic lattice of sodium chloride. From W. H. and W. L. Bragg, *The Crystalline State*, Bell, London, 1933.

The structure of diamond was found to confirm the organic chemist's concept of the four-valency of carbon, directed tetrahedrally in space, each carbon atom occupying a position central to four neighbors distributed around it at the corners of a regular tetrahedron and at distances of 1.54 Å units (Fig. 2). That the architecture of the crystal reveals its properties is well illustrated by the case of graphite in the same diagram. Here the atoms were found to be arranged in flat plates of hexagonal rings each atom in the ring at the same distance (1.42 Å) from its neighbors. These plates, however, in contrast to the case of diamond, are relatively far apart, 3.25 Å or over twice the spacing of adjacent planes in diamond. It is between these planes that the attractive forces are smallest and it is along these planes that the well-known cleavage of graphite occurs. Flaky, aromatic crystals such as benzene, naphthalene and anthracene possess these same hex-

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agonal ring planes with the same dimensions. Paraffins, aliphatic hydrocarbon chains, possess the carbon-carbon distance 1.54 \AA found in diamond.

surfaces, measuring the area covered, Langmuir could deduce the cross-sectional area and, hence, the length of the hydrocarbon chain. These experiments proved independently that each carbon atom in the chain was at the diamond-distance, 1.54 \AA from its neighbors, and that the whole chain was the zig-zag arrangement that the concept of the tetrahedral carbon atom would demand.

ELECTRON DIFFRACTION OF MOLECULES

The developments of quantum theory taught us the dualistic nature of light, its behavior in certain circumstances as waves, its atomistic nature as units or quanta of light in other circumstances. The application of this dualistic concept to matter in the early 1920's led to the consideration of matter not only as particulate or atomistic but also as waves and this in its turn led to the striking experiments, by Davisson and Germer and independently by G. P. Thomson, using electrons where X-rays had previously been used and, from the pattern of the electron reflections and diffraction, confirmation was obtained of the unitary structure of matter. The principal advantage deriving from electron diffraction experiments is that it has permitted the study not only of crystals but of liquids and, what is of still greater importance, the study of the atomic structure of gases and vapors. By means of such measurements we now have a large body of experimental data on the position of atoms in molecules, their distances one from another and the angles between the different constituent atoms in the molecule. We thus have from X-rays and electron diffraction studies, supplemented by a large body of data from the study of band spectra of molecules, a most detailed body of knowledge concerning the sizes of the individual atoms in molecules and ions in crystals as well as the variations in the atomic distances with changes in the manner in which these atoms are linked together.

The diagrammatic representation of these crystal and molecular structures usually presents a lattice framework, the centers of gravity of the atoms represented by circles or points and these joined by lines of length corresponding to the known atom distances. Actually it is now known that the atoms or ions enter into the structure as if they were spheres of definite size. To each atom or ion may be assigned an atomic

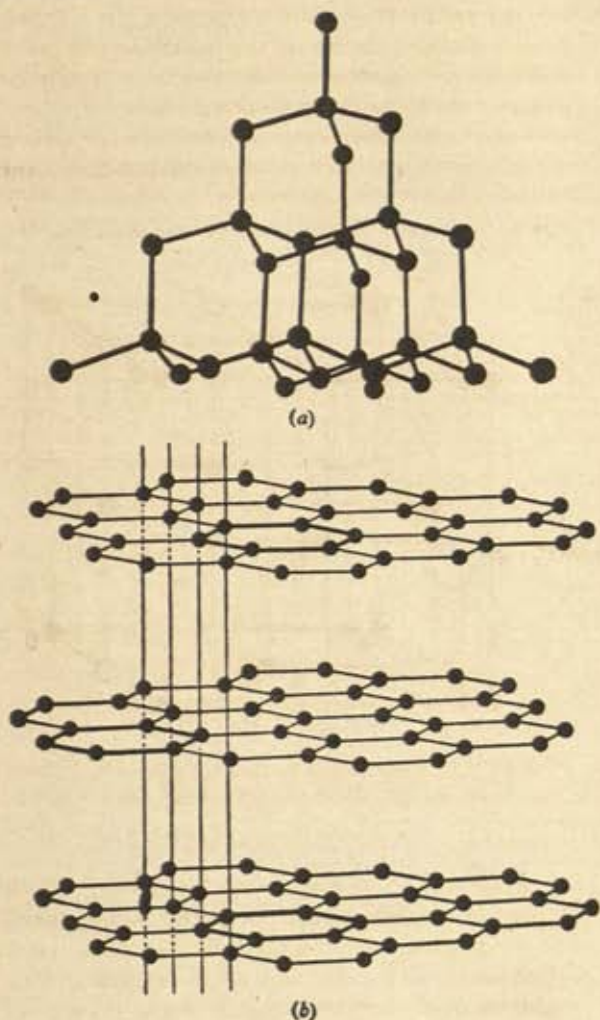


FIG. 2. Diamond and graphite structures. From W. H. and W. L. Bragg, *The Crystalline State*, Bell, London, 1933.

This conclusion from X-ray analysis found a very striking confirmation in the beautifully simple experiments of Langmuir on the areas covered by fatty acids spread as a monolayer, a layer of single molecules, on the surface of water. Fatty acids are long chains of hydrocarbons with a polar ending, COOH . The polar end is attracted to the water surface and the hydrocarbon chain is oriented out of the water and at a slight tilt from the vertical. By spreading known volumes of these fatty acids on water

or ionic radius, the distance between two centers being equal to the sum of the two radii. On this view the crystal or molecule becomes a close, ordered arrangement of spherical units the sizes of the units determining the geometry of the whole crystal. The forces that hold the units together vary. In inorganic crystals, such as sodium chloride, the bond is frequently ionic in character, the electrical attractions between oppositely charged particles being the most important binding forces. In other structures, the bond is a valency bond, the so-called co-valent bond, as in diamond, electrically neutral atoms being held by the same valency forces that hold atoms together in molecules. Other crystals, for example those of dry ice, are held together by neither ionic nor valency bonds, but by the weaker forces, the van der Waals forces, that hold molecules together. It is the molecules rather than atoms which are built into the geometrical structure. Such crystals have relatively low melting points and boiling points, as is well illustrated by dry ice. Most metals and alloys form structures of close-packed spheres of positively charged metal ions in which the free electrons, that give the metallic characteristics of heat and electrical conduction, are freely moving.

STRUCTURES CONTAINING SILICON AND OXYGEN

Let us put on our atomic spectacles, now, and look at some of the structures that arise from the linking of atoms together in architectural patterns dominated by well-defined and ascertained rules of structure building. First of all we shall examine some of the possibilities that arise when the two very common elements in nature, silicon and oxygen, interact. We choose this as our starting point for several reasons: first, because only two types of atoms are involved; secondly, because they interact according to a very simple rule and yet are able to produce patterns of structure with which we are all familiar, which confer valuable properties on the materials so constructed; and lastly, these structures may be used as type-illustrations of systems much more complex in composition and of great importance in organic and biological systems.

Silicon is always found between four oxygen atoms.

(a) As an independent group, SiO_4 , tetrahedral in structure, we find it associated as a nega-

tive ion, having four negative valencies, with metal ions in various silicates, *e.g.*, Forsterite, $\text{Mg}_2(\text{SiO}_4)$, Zircon, ZrSiO_4 , Garnet, $\text{Ca}_3\text{Al}_2(\text{SiO}_4)_3$, Topaz, $(\text{AlF})_2\text{SiO}_4$.

(b) It may form closed systems, two tetrahedra linked together by a common oxygen atom and thus in units of Si_2O_7 , or three in a ring with three common oxygen atoms in a unit Si_3O_9 , or six in a ring with six common oxygens in a unit Si_6O_{18} . This last unit is to be found in the beryl $\text{Be}_3\text{Al}_2\text{Si}_6\text{O}_{18}$.

(c) It may form endless chains and bands. The simplest type of chain is a string of tetra-

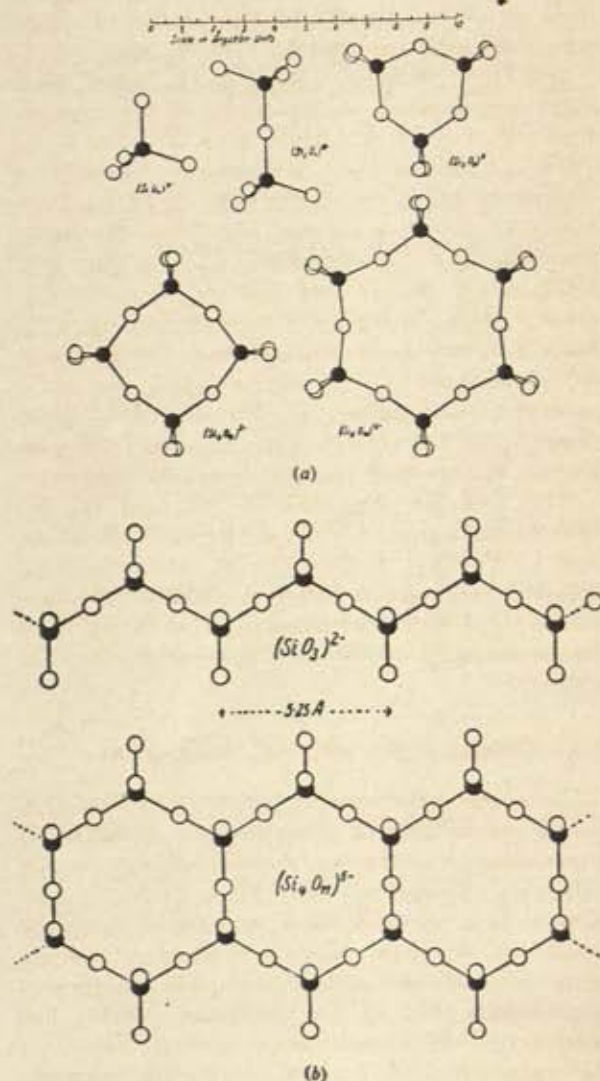


FIG. 3. Types of silicon-oxygen grouping in the silicates (a) Closed groups (b) Chains and bands. From W. H. and W. L. Bragg, *The Crystalline State*, Bell, London, 1933.

hedra linked corner to corner with an oxygen atom common to each linked tetrahedron. The composition of such a chain would be $(\text{SiO}_2)_n$. Two chains side by side and cross-linked would form a band. Minerals with these characteristic arrangements are fibrous in character. Asbestos is such a mineral. The long chains are bound together laterally by metallic ions.

These three types of linkage are illustrated in Fig. 3.

(d) Sheets of linked tetrahedra, each tetrahedron sharing three corners, with a sheet composition $(\text{Si}_2\text{O}_5)_n$, are present in laminar minerals such as talc and mica. They cleave readily, as does graphite, parallel to the planes of sheets which are held together by metallic ions.

(e) Three dimensional networks arise when each tetrahedron shares each of its corners. Pure silica is of this form with a composition $(\text{SiO}_2)_n$. Silicon may be partially replaced by aluminum, the resulting unit $(\text{Si}, \text{Al})\text{O}_2$ having a resultant negative charge, requiring the incorporation into the structure of metallic ions. Felspars are of this type and in the zeolites we have a silica-alumina structure so open that the basic ions may be withdrawn from the structure by replacement, a property made use of in permutit water-softening devices. The three-dimensional network may be cage-like, the well-known ultramarine pigment being of this type.

The linkages discussed in (d) and (e) are illustrated in Fig. 4. W. L. Bragg in England and L. Pauling in this country are largely responsible for our detailed knowledge of these structures which may assume great complexity. In the majority of them the crystals are ionic in character.

COMPLEX BIOCHEMICAL STRUCTURES

To attain structures of parallel complexity in which the binding is of a co-valent character it is necessary to turn to the realm of organic and biological chemistry. Here the capacity of carbon to link up with itself and other atoms in bonds of the usual valence type gives rise to structures, *in vitro* and *in vivo*, of a complexity outranking that of the inorganic world, the solution of which problems is even yet a matter for conjecture and the most fascinating research. In the simpler organic systems, by processes of breakdown and of synthesis, coupled with a most penetrating deductive effort, the structures have

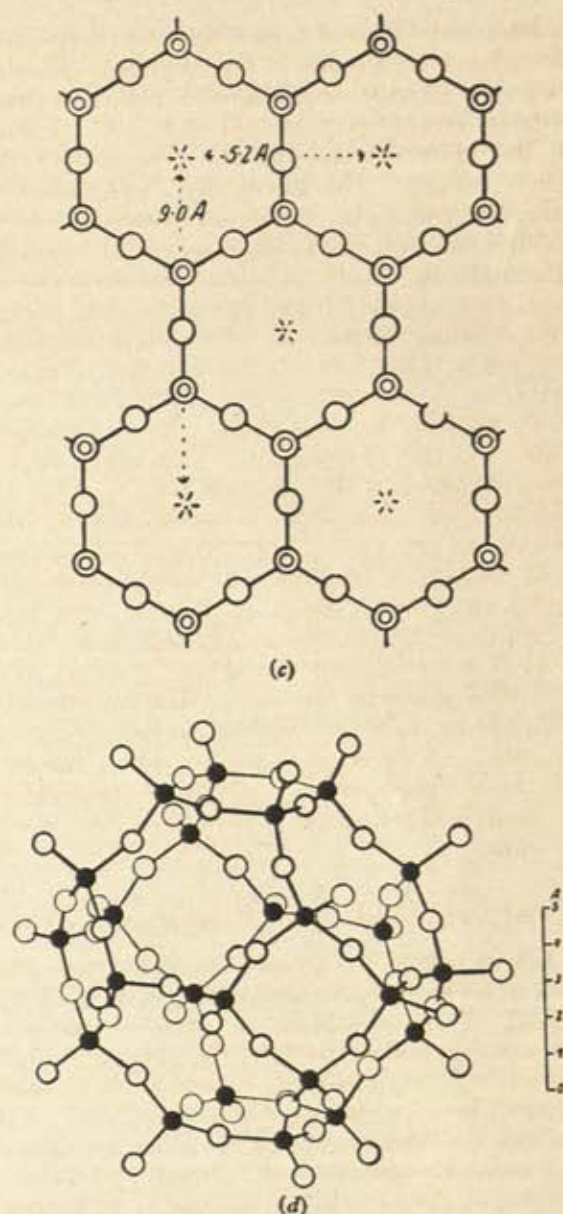


FIG. 4. Types of silicon-oxygen grouping in the silicates (c) Sheet (mica) (d) Three-dimensional net (ultramarine). From W. H. and W. L. Bragg, *The Crystalline State*, Bell, London, 1933.

been quantitatively decided. This is true even for the vitamins, the sterols and the hormones. In the more complex systems, both synthetic and natural, for example in the high-molecular weight synthetic resins and plastics, now so familiar, and especially in the more highly organized natural products such as rubber, cellulose fibers such as cotton, ramie and wood, starch,

fibrous proteins such as silk, wool and the muscle proteins, globular proteins such as egg albumen, haemoglobin and insulin, right up to such complex structures as the tobacco mosaic virus, with molecular weights ranging from the tens of thousands to many millions, we are only at the initial stages of solution of the problem.

MOLECULAR STRUCTURES FROM MODEL ATOMS

The ability to penetrate into the intricacies of such structures has been tremendously facilitated by the construction of atomic models based upon the findings of the X-ray, spectroscopic and electron diffraction data furnished by modern science as to the sizes of atoms and the included angles when assembled into molecules. From the determinations made upon hundreds of compounds, tables of data have been compiled from which atom-models of the correct dimensions with correct valence angles for particular valence states have been constructed. Recently such models have been introduced commercially by the Fisher Scientific Company with the coöperation of Professor J. O. Hirschfelder. They conform to the best data on atom-diameters, faces and angles between valence bonds and yield the correct relationships as to numbers of bonds per face and the planes in which they lie. With such atom models, even in the case of simple organic molecules, a much more instructive portrayal of molecular properties can be secured than is possible with the two-dimensional formulæ of earlier days.

With the various atomic units now available, including four types of carbon atom, two of oxygen, four of nitrogen, three of sulfur and one each of chlorine, bromine, iodine and hydrogen—the multiple forms for a given atom representing different types of bonding—it is possible not only to construct the simpler molecules with a few atoms but complex structures containing hundreds of constituent atoms. The linear scale of the atoms is so chosen that 1 cm. represents one Ångström unit (10^{-8} cm.) or a scale of 100 millions to one. One result of this choice of scale is that, with the aid of a centimeter rule the linear dimensions of the completed model can be rapidly measured with a reasonable degree of accuracy.

The atomic units, as purchased, are assembled and held together by the use of double taper pegs. While these are adequate for the assembly of the

simpler structures it has been quite generally found that larger molecular units do not possess an adequate degree of stability in handling subsequent to assembly. The weakness lies in the single valence bond pegs with the single central hole in each atom face. The double and triple bond assemblies with two and three hole-peg connections appear to be adequate. The inadequacy of the single bond hole-peg connection is the more evident because it is around such single bonds that the complex and simultaneous rotations of the molecules occur. Much important information concerning these intramolecular motions can be obtained by a study of the motions of the structural model.

A NEW METHOD OF LINKAGE FOR ATOMIC MODELS

The difficulty associated with this feature of the models has been successfully removed with a device developed by the writer recently in Princeton. Models containing hundreds of atoms have been constructed and subjected to manipulative test by his student, Mr. Bernard Becker, with most interesting results in the field of complex polypeptide and other structures. For the single bond peg we have substituted snap-fasteners of the type familiar in dress-making. Into each face of an atom model carrying the one-hole single valence we have bored a one cm. hole and into each such hole have driven the female end of a 1 cm. snap fastener, to a depth below the atom face equal to the thickness of the male half of the snap fastener. Two atom faces thus provided can then be linked together in a firm linkage by soldering together, back to back, two male portions of the snap fastener and inserting the unit so constructed in the two female units in the two faces. Accurately constructed, these give a most satisfactory single valency bond. They permit a much greater freedom of rotation about the bond than is possible with the hole-peg device while the stability during manipulation of molecular models so constructed is of an entirely higher order of excellence. Long polypeptide chains have been subjected to elaborate studies of folding possibilities without any collapse of the structure and with complete freedom of single bond rotation. Our earlier efforts with the hole-peg assembly always led to disruption of the structure. So modified, the Fisher-Hirschfelder molecular models can be a much more faithful

picture of the dynamic entity that a molecule must be. Even with relatively simple structures such as the hydrocarbons, butane, pentane and hexane, the snap-fastener single valence permits a much more effective study of the steric relationships involved. Recent research has shown that the rotation around single bonds is not entirely unrestricted, as early theories of organic chemistry demanded. The new molecular models offer the possibility of studying the phenomena involved more intimately than with the types of model used hitherto.

THE STRUCTURE OF FIBROUS PROTEINS

The X-ray evidence in the field of the proteins is most definite in the case of the fibrous proteins. With the silk protein, fibroin, and the hair protein, keratin, precise knowledge is available concerning certain details, while in others there is much that is still indefinite. The data on silk fibroin, which is one of the simplest proteins, are in best accord with the view that silk fiber consists of long filaments of fully stretched polypeptide chains lying parallel to the fiber axis. The repeating unit occurs every 3.5 Å units and the constituent peptides are mainly those of the amino-acids, glycine $\text{CH}_2\text{NH}_2\text{COOH}$ and alanine $\text{CH}_3\text{CHNH}_2\text{COOH}$. These are among the simplest of the amino-acids and, hence, the side chains, R, which appear at right angles to the plane of the polypeptide chain are H and CH_3

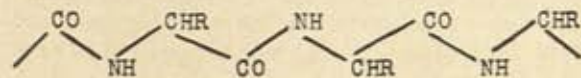


FIG. 5. The extended polypeptide chain.

respectively and therefore occupy relatively small areas along the chain.

Hair and wool protein or keratin possesses a property which distinguishes it sharply from silk fibroin, namely its large capacity to stretch and its elasticity. It is now known to exist in at least three forms. One of these, β -keratin, obtained by simple stretching of the hair, most closely resembles the silk fibroin. Its X-ray analysis suggests that it also is an extended chain of polypeptide units in which the side chains are more complex than in silk. The repeating unit in the "backbone" of β -keratin occurs every 3.33 Å units. Individual polypeptide chains are spaced 10 Å units apart which is the average distance

required by side chains (which, however, show quite unequal lengths) normal to the backbone issuing from each chain. These side chains are both acidic and basic and may thus mutually saturate each other. Some of the connecting links between backbone chains are cystine molecules which account for the well known sulphur content of these proteins. In the β -keratin there is another spacing of about 4.5 Å units and this is regarded as the distance of separation in the third dimension of the polypeptide chains.

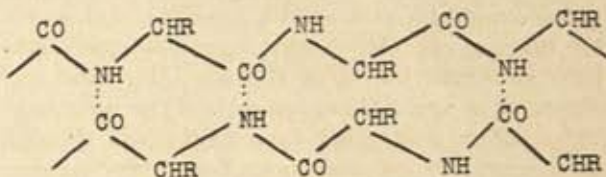


FIG. 6. Hydrogen bonded polypeptide chains.

(The R groups must be thought of as projecting alternately above and below the plane of the paper.)

It is assumed by many that successive chains in this dimension are held together by so-called hydrogen bonds $\text{N}-\text{H}\cdots\text{O}-\text{C}$.

The stretched form or β -keratin is not, however, the normal form of hair keratin. Normal or α -keratin must be a folded structure. It is these folds which are drawn out when the fiber is stretched and the stretched condition may be "set" by exposure to steam heat while the tension is maintained. It is this process of "stretching" and "setting" which has attained the dimensions of a fine art, common to both sexes, in the "permanent wave" and "set" and in the "trousers crease". As is also well known to both sexes, this imposed change is only temporary, the hair or wool reverting gradually to its normal folded α -keratin structure.

The work of Astbury and his co-workers on α -keratin has revealed that this folded configuration may be derived from fully extended β -keratin peptide chains by assuming that the main chains contract to about one half of their original length, three peptide chains occupying 5.1 Å units or approximately one half of the 3×3.33 Å units in the β -structure. The side-chain spacing is maintained at about 10 Å units. The backbone spacing does not seem to be any longer present. Astbury has himself suggested a method of folding the stretched polypeptide chain to give a folded or buckled grid in which the chains take up hexagonal configurations. Others have sug-

gested that such folding into hexagons involves intra-molecular change leading to closed hexagons and this idea was systematically developed by Wrinch into her "cyclol hypothesis" of protein structure. Hydrogen bonding is an alternative method of producing such hexagon closing. A year ago Neurath examined such proposals with the aid of models devised by Mack and reached the general conclusion that "unless unreasonable distortion of bond angles are assumed, these configurations are too condensed to permit residues (side chains), other than those of glycine and alanine and hydrogen atoms to get into the positions called for by the carbon atoms of the hexagonal rings to which they are attached." He further concludes that "from consideration of space requirements of amino acid residues it follows also that the cyclol structure is too condensed to permit the accommodation of side chains." The cyclol hypothesis and, by implication, Astbury's first-proposed structure for α -keratin have recently been severely criticized by Pauling and Niemann on these and other grounds. Astbury has himself quite recently accepted the conclusions reached by Neurath in the matter of space required by the side chains.

Some indications of the manner in which these difficulties might be surmounted are contained in the final sentence of Neurath's paper, "The question suggests itself, therefore, whether a contracted form of polypeptide chains may not be arrived at by evoking a three-dimensional folding of the main chains which would still preserve the alternate orientation of the side chains." Astbury himself remarks, "We must consider seriously now whether we ought not to accept once and for all at least the conclusion that the intramolecular folds of the proteins are in essence always of the β -type. Something like that is what the X-ray findings have been pointing to for a long time." In the final section of his paper he indicates that a possible manner whereby this may be achieved is now under study and that the results while still incomplete are promising.

MOLECULAR MODELS OF FOLDED POLYPEPTIDES CHAINS

The stable molecular models of polypeptide chains made possible by the "snap-fastener" single bonding described in earlier paragraphs produce the necessary flexible yet stable systems with which alternative mechanisms of folding of

β -chains may be studied. Mr. Bernard Becker has been able to show that there are types of folding which are at once compatible with the requirements of the X-ray data and still leave adequate spacings for the side-chain demands placed on such folded structures. Quite generally our experiments with the new flexible models reveal that we are as yet only at the beginnings of our knowledge of the manifold ways of folding such chains of polypeptides and that, in principle, there are many possible solutions.

The unit in a β -polypeptide chain is the sequence of groups $\text{CO}-\text{NH}-\text{CHR}$. This grouping, when the bond angles are properly located, is not far from a planar model. It is easy to show that such peptide units can be arranged in a continuous chain in which each unit is packed, back to back with other units, in what we may term the one up one down or filter-press configuration, as illustrated in Fig. 7. The three-

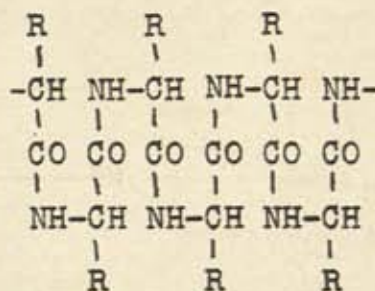


FIG. 7.

dimensional model of such a structure shows it to be possible and compact, with ample room for the side chains, R, which emerge at right-angles on alternate sides of the axis of the structure produced by the "filter-press type" arrangement. Measurement of this unit shows that it repeats every 4.5 Å units. This would not satisfy the dimensional requirements of α -keratin. It has, however, features that are both suggestive and instructive. It lends itself readily to double hydrogen bonding between adjacent chains.

We have already mentioned that attention has been directed to units of six peptides and that objections have already been raised to Astbury's suggested method of folding and the Wrinch "cyclol-6" unit. The type of folding just described can be bent to give a closed 6-peptide unit. A triangular prismatic unit is produced having quite definite interest. Inspection shows that there is a repeating triangular pattern in the

structure. The side-chain bonds on top form a small triangle, the CO groups a large triangle. On the bottom side the side-chain bonds form a large triangle and the CO groups a small triangle. Similar conditions obtain with the NH groupings. On top and bottom there is ample space for any conceivable array of side chains. By bringing such six-peptide units into conjunction with one another so disposed that adjacent units are, alternately, top meeting bottom and vice versa at the triangle corners, geometrical patterns of 6-peptide units can be produced. The configuration at the angles is such that CO in one is adjacent to NH in the next and vice versa. Such units then can tie together by the "hydrogen-bonding" association so frequently postulated in protein structures. It is easy to show, however, that the triangular pattern can be developed with a continuous —CO—NH—CHR— linking by crossing over at the angle of the triangles with a CO-NH linkage between groups in the two triangles as in Fig. 8. We have constructed

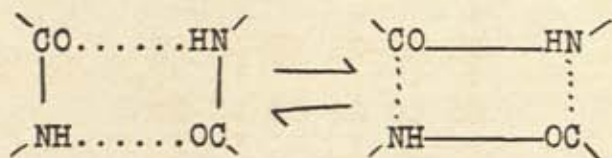


FIG. 8.

symmetrical arrangements of such triangular 6-peptides to give the 96-peptide unit. The next larger symmetrical unit of this pattern would contain the much discussed 288-peptide unit which is the estimated size of a number of globular proteins in the 35,000 molecular weight range. So long as such patterns are planar there is no difficulty as regards accessibility of and adequate space requirements for a normal sequence of side chains.

The 6-peptide structure just considered suggests at once that a 3-peptide can be equally well arranged in a closed unit. The side chains can be disposed in two ways either projecting outwards at 120° angles in the plane of the structure or vertically to that plane. Both of these structures can be arranged in geometrical patterns with the side chains as the connecting links in the former and hydrogen bonding or CO-NH linkages in the latter. In this latter case, cage structures may be produced with the side chains projecting vertically from the cage faces. Two such tripeptide closed structures placed back to back give a "ham-sandwich" structure with the

NH groupings the "ham" between the two CO-CHR "bread" layers.

A MOLECULAR MODEL FOR NORMAL HAIR FIBER

What is apparently of greater significance, however, is that a 3-peptide fold of an indefinitely long peptide chain can yield a folded spiral. The three dimensional model thus obtained derives from the planar structure of the previous paragraph and has many highly satisfactory features. Thus, the keto-groupings arrange themselves in 3 linear arrays making 120° angles with the central axis of the fold. The same is true of the NH groupings and the side chain bondings. Inspection shows that, in the case of these latter, there is again ample room for normal side-chain sequences. Measurement shows that this particular method of fold gives accurately the spacing characteristics required by Astbury for the normal folded-hair or α -keratin structure. The repeating unit has quite accurately a 5.1 Å unit spacing. The side-chain distances as with β -keratin would average about 10 Å. Stretching this folded structure would give the 100 per cent extension demanded by the properties of hair-fiber and the result would be the β -keratin structure. It obviates the difficulty arising in connection with earlier proposals as to folding which required that all the R-groups of the side-chains be either "on the top or the bottom of the chains where there is insufficient room to accommodate them" (Bull). In our model Fig. 9(a) and 9(b), also, there is a favorable disposition of the side-chains to exercise that interaction with one another which must play a role in determining that keratin exists in the contracted α -form whereas silk fibroin whose side-chains are typically non-polar does not show the tendency to form the α -type fold. Our 3-peptide folded spiral therefore reproduces with great fidelity the demands of our present knowledge as to the α -keratin structure, including the disappearance of the 4.5 Å unit spacing. It represents, therefore, one possible solution for this structure. In the keratin group are included, in addition to the hair fibers, the protein of bird feathers, nails, claws and porcupine quills.

OTHER ALTERNATIVE FOLDINGS OF EXTENDED HAIR FIBER

We have examined an alternative folding of the peptide chain which also yields the 5.1 Å

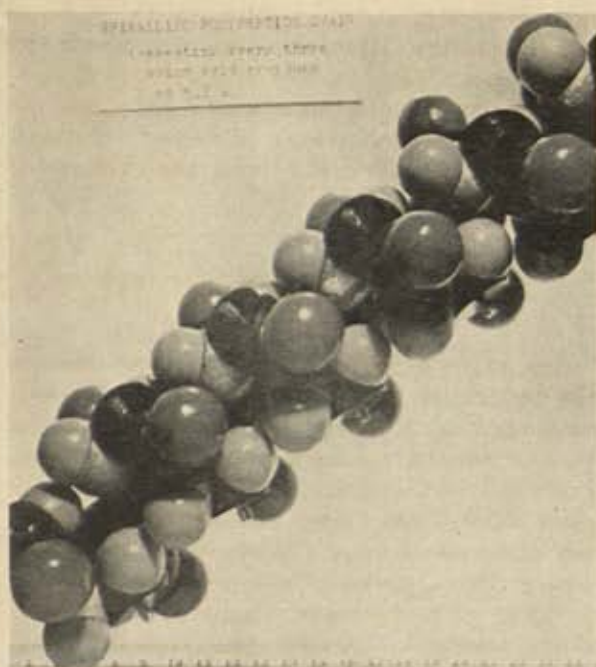


FIG. 9a. Spirally folded polypeptide chain.

The skeleton of a hair or wool fiber, seen through atomic spectacles, would appear somewhat like the model on the left, which represents, as printed, a magnification of about 50 million diameters. It is a spiral fold of units each containing the atom sequence $-\text{CO}\cdot\text{NH}\cdot\text{CHR}$. There are three such units in each turn of the spiral. The R-groups, known as the side chains, are not included in this photograph. They would be attached to the fiber at the posi-

repeating unit. We have characterized this as the one up-two down fold illustrated graphically in Fig. 10. We do not regard such a structure, although free from major objections, to be so satisfactory as the one just considered since it causes a close association of two out of three side chains of a sequence along one face of the spiral and at 3.5 \AA units apart. These positions would accommodate side chains which are not unduly large and permit larger side-chain units to be accommodated on the remaining side-chain position.

We are convinced from experiments with our flexible peptide chains that the conclusions of Neurath with respect to the non-spiral type of folding suggested by Astbury cannot be considered final. Our own trials have indicated the definite possibility of a planar folding with adequate side-chain spacing involving however a definite angular displacement from cis- and trans-folding at the single bonds in the chain.

As is well known, hair keratin exists in another

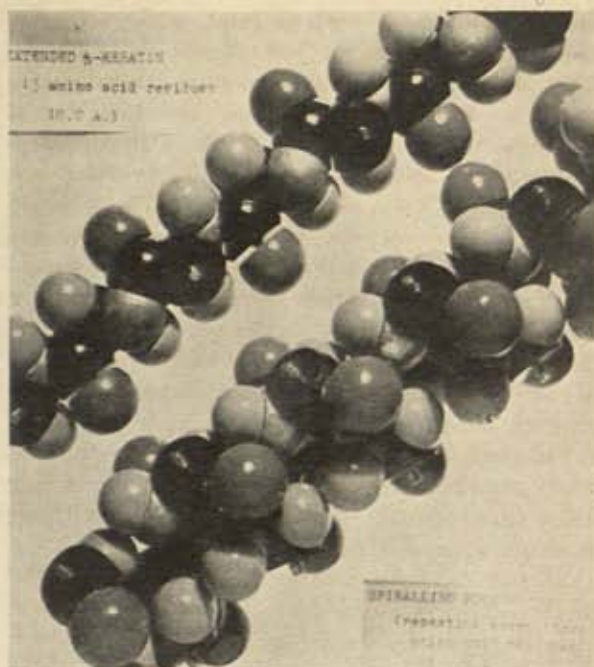


FIG. 9b. Comparison of spiral fold with extended chain.

tions shown by the bevelled pegs in the model. On subjecting this model to tension it will stretch to 100 per cent of its own length to give the stretched or extended form, as do hair and wool fibers. This stretching is assisted by heat and steam. It is hair so stretched which can be "permanently waved" or "set." The "trousers' crease" is also applied to the stretched wool fiber. Both the normal and the extended fibers are shown in the photograph on the right.

state, the "super-contracted" form. It assumes this form after being stretched and treated with heat and moisture for a short time; if it is then allowed to contract, it will contract to a shorter length than the normal α -form. The X-ray analysis does not reveal any new definite repeating pattern for this form. Experiments with our flexible β -chains indicate that spiral folding can be achieved with units of 4, 5 and 6 peptides

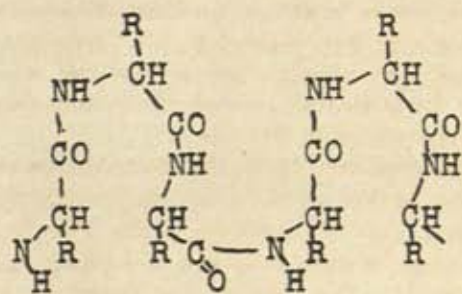


FIG. 10.

in a single spiral fold without any particular difficulty as to disposition of side chains save that the space available becomes progressively smaller. It is obvious that such spiralling would produce contracted forms of the keratin considerably shorter than the α -form. It would probably yield a 5.1 Å unit distance. There is no evidence, however, that would compel the formulation of such a spiral interpretation of the super-contracted state. There is in the judgment of certain workers some evidence that what is achieved in the production of super-contracted keratin is a randomly folded and randomly arranged keratin chain. Our folding experiments definitely indicate the possibility of this since we have examined many other patterns of folding than those already discussed in detail without noting insuperable difficulties. It is well known that the random folding of rubber from the stretched, crystalline form, to a normal form only 10 per cent the length of the stretched chain must involve a high degree of random folding.

MYOSIN AND COLLAGEN FIBERS

The protein of muscle, myosin, as Astbury has emphasized, is found to have the extension and contraction characteristic of hair fiber, with, according to Astbury, the α -configuration as the normal resting state, the super-contracted form as the contracted tissue and a possible extension to the β -form with tension. In muscle tissue the contraction and return to the normal state are chemically induced. The absence of cystine linkages in myosin probably facilitates the attainment of the super-contracted state whereas these "vulcanizing" linkages in keratin tend to prevent this in hair. In the collagen-group fibers of connective tissue the presence of proline as an important constituent amino acid modifies the attainable extension. We have shown that proline can be built into such amino-acid chains. As Astbury has suggested, the presence of a partially cis-configuration in the fold may account for a smaller peptide dimension that has been postulated in this case.

It is apparent, from the complexities of the problem in the case of the fibrous proteins already outlined, that the problem of the globular proteins must be essentially one of a higher order of complexity. We will content ourselves, therefore, with the observation that it is possible that

there is no single unique solution of the globular protein problem, that the ease with which the polypeptide chain can fold into units of 2, 3, 4, 5, 6 and even higher numbered folds offers the possibility of very many different solutions. Progress to finality will involve the exploration of many pathways of inquiry.

MOLECULAR MODELS OF SYNTHETIC STRUCTURES

The examination of the polypeptide chain in the production of protein structures represents one important section of the problems that can be examined with the new molecular models. Preliminary excursions into other fields have already been made. They are instructive in the field of chemo-therapy. We have photographed, among others, models of sulfanilamide and sulapyridine. The hormone, thyroxine, is an interesting structure. Among the vitamins, vitamins A, B₂, B₆, nicotinic and pantothenic acids, vitamin E and K₁ make interesting models. In the sterol group, models of cholesterol, cholestanol and coprostanol serve to check data on molecular dimensions of these large molecules. In the models of carcinogenic substances of the benzantracene and benzphenanthrene types there appears to be some correlation between activity and planar and non-planar configuration of the molecules. In the field of three-dimensional synthetic polymers of the plastic field the molecular models are especially useful in indicating structural arrangements. Polystyrene and lucite polymers are illustrative of these.

Paralleling the protein field there is a similar area of study in the carbohydrate field. The polyoxymethylene and polymethylenes give fibrous structures. The cellobiose unit builds up into the structures of cotton and wood cellulose and the gluco-pyranose group into the starch molecule. The nature of the repeating units and of the linkage between them is now under active study. Synthetic fibers are derived from cellulose in acetate and viscose rayons. More recently nylon takes its place as a synthetic linear polymer prepared by condensation of a diamine and a dibasic acid condensed into a chain of indefinite length. In the field of natural and synthetic rubbers there are analogies to the protein problem that we have discussed in detail. The stretched rubbers are crystalline and are

known to be extended chains. On release of tension these chains fold to give the normal state of the substance. Experiment shows that folding similar to that in the polypeptides is easily possible, but the final structure undoubtedly contains an extensive randomness of fold showing no X-ray pattern. In rubber, also, the process of vulcanization establishes cross linkages between the hydrocarbon chains and thereby decreases the natural characteristics of the rubber molecule. The exploration of any given field brings a multiple reward in the increasing knowledge gained not only in the field investigated but in all the other parallel fields of study.

ACKNOWLEDGMENT

A final word of indebtedness to the author's pupil, a Princeton Senior, Mr. Bernard Becker, is here expressed. Of him it may be said, to adapt the lines of Francis Thompson in "Her Portrait", "And teaching him, by his ingenious art, the master threefold learns for all he can impart." Mr. Becker has learned to manipulate the atomic models here discussed so skillfully that they have revealed to both of us very much more than either of us could ever have anticipated and have provided us with the equivalent of more efficient atomic spectacles with which to observe large molecules.

CRYSTALLINE DIPHTHERIA ANTITOXIN¹

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(Read April 24, 1941)

ABSTRACT

Diphtheria toxin forms a precipitate when mixed in certain proportions with serum from a horse which has been immunized against the toxin. This precipitate is a compound of the toxin and antitoxin. The compound is dissolved in slightly acid solution and the toxin digested by trypsin. The antitoxin remains in solution. About 30-60 per cent of the original antitoxin may be recovered in this way. This "crude antitoxin" may be further separated into three fractions by precipitation with ammonium sulfate at about pH 7.2.

The fraction soluble in 0.35 saturated ammonium sulfate but insoluble in 0.65 saturated ammonium sulfate has a high antitoxic titer (700,000-1,000,000) antitoxin units per gram protein nitrogen; 90 per cent or more of the protein is precipitated by diphtheria toxin. It is strictly homogeneous in the ultracentrifuge with a sedimentation constant of 5.7×10^{-12} . It shows only one boundary at pH 7.3 in the electrophoresis cell but there is some reversible spreading. This fraction corresponds probably to the highly purified preparations of Pope and of Pappenheimer and their collaborators.

Solubility determinations show that this fraction is still quite inhomogeneous. Extraction of this fraction with 0.5 saturated ammonium sulfate at pH 7.2 yields a small amount of a protein which has constant solubility and is therefore probably a pure protein. This protein crystallizes readily in the form of poorly formed thin plates. The antitoxic value is unchanged after three recrystallizations.

VANBEHRING and Kitasato in 1890 found that the sera of animals which had received repeated small doses of diphtheria toxin developed the property of neutralizing the poisonous effects of the toxin. This neutralizing substance was called antitoxin. Diphtheria antitoxin was the first such substance discovered and is still one of the most powerful therapeutic agents known. Further study of diphtheria and other antitoxins has shown that they are proteins closely related to the normal serum proteins. They must possess some characteristic chemical structure, however, not present in the normal proteins since they neutralize toxin whereas normal serum proteins do not. Knowledge of the structure responsible for the antitoxic power may eventually lead to the synthesis of antitoxins of

greater therapeutic value. The first step in the attempt to identify the structure responsible for this therapeutic value is the isolation of the antitoxin in pure form. Preparations of pneumococcus antibody, which are pure in the sense that they are completely precipitated by antigen, have been obtained by Chow and Goebel (1935), Chow and Wu (1937) Heidelberger and Kendall (1936) and their coworkers. Petermann and Pappenheimer (1940) prepared diphtheria antitoxin which was homogeneous by electrophoresis or ultracentrifuge but was not completely precipitated by toxin. Highly purified preparations of diphtheria antitoxin have also been obtained by Pope and Healey (1939) and coworkers.

Ramon (1922) showed that under certain conditions diphtheria toxin and antitoxin combine to form an insoluble precipitate. Evidently recovery of the antitoxin from this precipitate would result in a very considerable purification. Ramon was able to recover some antitoxin from this precipitate by heating in slightly acid solution (Ramon, 1923). Pope (1939) found that most of the antitoxin could be recovered from such precipitates by treatment with pepsin in slightly acid solution and the work has been confirmed and extended by Pappenheimer and coworkers. Pepsin destroys both toxin and antitoxin to some extent and it seemed possible that better yields might be obtained by using trypsin. It was found that trypsin has no effect on the toxin-antitoxin in neutral solution but if the complex is dissolved in dilute acid and then brought back to neutral solution the toxin is digested and 30-60 per cent of the antitoxin may be recovered.

It was thought at first that this result was due to dissociation of the toxin-antitoxin complex in acid followed by digestion of the toxin. It appears, however, that this is probably not the case since diphtheria toxin is very unstable in acid (pH 3.5) as Pappenheimer (1937, 1938) showed, and would be inactivated and precipitated were it present in solution. This does not occur when the toxin-antitoxin complex is al-

¹ The experimental results will be described in a forthcoming number of the *J. Gen. Physiol.*

TABLE I
OUTLINE OF A METHOD OF PREPARATION OF CRYSTALLINE DIPHTHERIA ANTITOXIN

33 liters toxin + 4 liters antidiphtheria plasma, 24 hours 20° C. Filter.			$2 \times 10^6 L_f$	20 L_f/PN
Filtrate	↓	Precipitate		
Suspend in 5 liters M/10 KH_2PO_4 titrate to pH 3.7, add 2 gm crystalline trypsin 25° C. 20 hours. Titrate to pH 7.2 25° C. 24 hours. Filter.				
Precipitate	↓	Filtrate	$6 \times 10^5 L_f$	350 L_f/PN
Adjust to 0.33 sat. ammonium sulfate and filter.				
Precipitate	↓	Filtrate	$4 \times 10^5 L_f$	500 L_f/PN
Adjust to 0.45 sat. ammonium sulfate and filter.				
Precipitate	↓	Filtrate	$2 \times 10^5 L_f$	700 800 L_f/PN
Adjust to 0.65 sat. ammonium sulfate and filter.				
Filtrate	↓	Precipitate		
Stir + 3 liters (0.5 sat. ammonium sulfate, 0.05 M pH 7.4 phosphate). Filter.				
Precipitate	↓	Filtrate	$1.5 \times 10^5 L_f$	700 800 L_f/PN
Titrate to pH 3.5. Filter.				
Precipitate	↓	Filtrate	$1 \times 10^5 L_f$	700 800 L_f/PN
Titrate to pH 7.0, add sat. ammonium sulfate slowly till very slight silky precipitate forms. Stand 6° C. 24 hours, centrifuge.				
Supernatant	↓	Precipitate		
Fine plates, needles and some amorphous. Suspend in 50 ml 0.5 sat. ammonium sulfate, add water till clear, add sat. ammonium sulfate till slightly cloudy, 25° C. 2 hours. Irregular plates, no amorphous. Centrifuge.				
Supernatant	↓	Precipitate	$6 \times 10^5 L_f$	700 800 L_f/PN
Dissolve in 5 ml water and sat. ammonium sulfate slowly till slight turbidity. 25° C. 1 hour. Thin plates.				

lowed to stand in acid. The action of trypsin does not take place in acid but during and immediately after neutralization. It seems probable that the toxin-antitoxin complex dissolves as such in acid and the toxin is then split off by the trypsin during and after neutralization while the complex is still dissolved. If the toxin-antitoxin complex is allowed to precipitate again in neutral solution before the addition of trypsin, the toxin is no longer digested.

The "crude antitoxin" recovered after removal of the toxin contains 30-60 per cent of the original total antitoxin.

The preparation is 95 per cent or more precipitated by toxin and has an antitoxin titer of 300-400 units² per mg protein nitrogen. This

²One antitoxic unit is defined as the equivalent of a "standard antitoxin unit" and is approximately equivalent

preparation may be further purified by precipitation with ammonium sulfate (Table I). The fraction precipitating between 0 and 35 per cent saturated ammonium sulfate has an antitoxic value of about 550 units per mg protein nitrogen while that precipitating between 0.45 and 0.65 saturated ammonium sulfate has an antitoxic value of 700-800 units per mg protein nitrogen by the flocculation test.

The antitoxin value of this purified antitoxin, as determined by animal protection tests, has been determined by Dr. W. E. Bunney at E. R. Squibb and Sons, New Brunswick, N. J. Two preparations were tested and found to contain about 700 antitoxin units per mg protein nitrogen.

to the quantity of antitoxin which will neutralize 100 times the quantity of toxin required to kill a guinea pig in 5 days.

This fraction probably corresponds to a similar preparation obtained by Pope and Pappenheimer by means of pepsin digestion. It is homogeneous by electrophoresis and ultracentrifuge measurements. The solubility of this fraction, however, is not constant but varies with the quantity of solid present showing that it consists of two or more proteins which are indistinguishable by electrophoresis, rate of sedimentation or precipitation by toxin.³ The fact that the solubility varies with the amount of solid present shows that the solid phase in the dilute suspension is different from that in the more concentrated. A partial separation of the system has therefore been accomplished and, on paper at least, all that is necessary is to repeat the process until no difference in solubility is observed. This is the theoretical basis for the fact that fractional precipitation has been of such great practical value in the purification of proteins.

In practice it is not always possible to complete the separation in this way owing to the fact that insufficient material is available or because the protein is too unstable and changes during the experiment. In the present case both difficulties are encountered. Nevertheless, it is possible to obtain a much more homogeneous protein by removing only the most soluble portion of the preparation. This is best done by extracting the solid precipitate with half saturated ammonium sulfate at pH 7.2. The protein obtained in this way is much more nearly homogeneous but still does not have constant solubility. Repetition of the extraction with this fraction would be expected to result in further improvement but the yield is so small that this cannot be done in practice. If this saturated solution is titrated

to pH 3.5, however, a precipitate appears. After removal of this precipitate the protein has constant or nearly constant solubility and crystallizes readily in rather poorly formed thin plates (Fig. 1). These plates are slightly double refractile. They are slightly less soluble than the amorphous protein and their appearance in solution is greatly accelerated by inoculation of a supersaturated solution with some of the plates. They resemble very closely the first crystals of ribonuclease obtained by Kunitz. Ribonuclease crystals, however, become beautifully formed on recrystallization or on long standing while the antitoxin crystals do not improve and may become less well formed. This difference is due to the fact that the antitoxin is very unstable. Even after 24 hours at 20° C. some less soluble protein has been formed and after a few days the solubility curve of the preparation resembles that of the crude fraction from which it was derived. At the same time the flocculation time, when the antitoxin is mixed with toxin, increases although the final endpoint remains the same. The formation of this less soluble protein interferes with crystallization and soon prevents it altogether.

Similar changes in the rate of flocculation with aging have been noted by Glenny and others with antitoxic sera. It is possible that the pure antitoxin represents the protein in its original form and that the more insoluble proteins are derived from this unstable protein. So far no conditions have been found which prevent these changes.

Properties of the Antitoxin.—Purity. The electrophoretic pattern has been determined by Dr. A. Rothen. There is only one boundary but there is considerable "reversible spreading" in dilute phosphate buffer at pH 7.3. A possible cause of this phenomenon, which has been noted with several proteins, is the migration of water in the cell due to electroendosmosis. If this were the cause the spreading should not be observed under conditions which prevent the electroendosmosis. The experiment was therefore repeated in the presence of calcium chloride at pH 7.3 and at pH 3.0. Glass has no charge when in contact with these solvents and hence there is no electroendosmosis. There is no reversible spreading of the protein under these conditions.

The protein is strictly homogeneous in the ultracentrifuge with a sedimentation constant of $S_{20}^{\text{water}} = 5.3 \times 10^{-12}$. The diffusion coefficient is $D^{20} = 5.56 \times 10^{-7}$ cm²/sec and the molecular weight calculated from these figures is 90,500

³ This result is simply another example of the fact that the solubility method, which is theoretically identical with the classical melting point method, will distinguish between closely related proteins which are indistinguishable by other methods. Thus Landsteiner and Heidelberger found that hemoglobin from donkey and horse could be distinguished by this method although serologically they are extremely similar. Crystalline pepsin (Herriott, Desreux and Northrop, 1940) prepared without special purification, is strictly homogeneous by electrophoresis or ultracentrifugation but does not have constant solubility and may be shown to contain several different proteins. Mixtures of samples of chymotrypsinogen of different solubilities are indistinguishable by electrophoresis (Butler, 1940) as are mixtures of pepsin and iodinated pepsin (Herriott, 1941) although in the latter case the solubilities are very different. Egg albumin from closely related species is also indistinguishable by the electrophoresis technique although they may be distinguished by serological tests (Landsteiner, Longworth and van der Scheer, 1938).



FIG. 1. Crystalline diphtheria antitoxin.

(Rothen, in press). This is close to the figure obtained by Pappenheimer for a sample of antibody obtained by the action of pepsin. Purified antibody prepared by heating the toxin-antitoxin complex in acid has a sedimentation constant of 6.8×10^{-13} . Apparently, therefore, trypsin hydrolyzes part of the antitoxin molecule as well as the toxin. This agrees with Pappenheimer's experiments with pepsin.

The most highly purified fraction has nearly constant solubility. All the preparations of this fraction give better solubility curves than most proteins but only one shows really constant solubility. These curves, however, were all made on amorphous preparations and hence are open to some uncertainty as it is not possible to be sure that they represent equilibrium values. The crystalline preparations do not give as good curves owing to the fact that some less soluble material is formed while the crystallization is taking place.

The protein contains about 2.5 per cent carbohydrates determined as glucose by Sorenson's method.

PRECIPITATION OF PURIFIED ANTITOXIN AND TOXIN

Solutions of various samples of purified antitoxin were mixed with an equivalent of crude toxin, obtained from E. R. Squibb and Company, or of purified toxin. The solutions were kept at 50° C. for 20 hours, centrifuged, and protein nitrogen determined in the supernatant. 4 to 10 per cent of the total protein nitrogen present remains in the supernatant with both the pure antibody having an antitoxic 800 L_i/mg P.N. and with the fraction precipitated between 0.35–0.45 saturated ammonium sulfate (400–500 L_i/mg P.N.) and with either crude or purified toxin. 90–95 per cent of the total protein nitrogen, therefore, precipitates out. It is not possible to say at present whether the protein nitrogen which fails to precipitate comes from the toxin or antitoxin.

This result indicates the presence of at least 2 antitoxins which combine with different amounts of toxin. Evidence for the existence of 2 such antitoxins has been obtained by Kekwick and Record (1941).

PRECIPITATION ZONE WITH CRUDE AND PURE ANTITOXIN AND TOXIN

Mixtures of immune serum and crude toxin precipitate only over a range of concentration in

which the two substances are present in the proportion of less than 2 to 1; that is, if complete flocculation occurs with a 1 to 1 mixture the precipitation will be incomplete if more than 2 equivalents of either component is present.

With pure antibody and crude toxin the range is about doubled and precipitation occurs over a range of 4 to 1.

With pure antibody and purified toxin (kindly supplied by Dr. A. M. Pappenheimer, Jr.) the range of complete precipitation is very wide and the components may be varied in the ratio of at least 64 to 1.

IMMUNOLOGICAL REACTIONS

Some of the immunological properties of the purified toxin have been determined by Dr. Carl Ten Broeck. The serum of a rabbit immunized against normal horse serum gave a precipitate with 1/4,000 ml normal horse serum (containing about 0.002 mg protein nitrogen) but gave no precipitate with 1 ml of a solution of purified antibody containing 1/10 mg protein nitrogen.

Guinea pigs sensitized with purified antibody reacted on injection of 0.05 mg antibody protein nitrogen, whereas 5 mg normal horse serum protein nitrogen was required to cause a reaction.

The purified antitoxin is, therefore, antigenically distinct from the normal serum proteins.

The toxin and the anti-diphtheria horse plasma used in this work were obtained from the Biological Laboratory of E. R. Squibb and Sons, New Brunswick, N. J.

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THE METHOD OF ACTIVATION OF MELANOPHORES AND THE LIMITATIONS OF MELANOPHORE RESPONSES IN THE CATFISH *AMEIURUS*

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ABSTRACT

In the skin of a pale catfish the large melanophores are represented by black spheres some 45 microns in diameter. In a fully dark catfish each such melanophore covers an area with a diameter of some 145 microns. The concentrated state of the melanophores is induced through nerve fibers that presumably discharge adrenaline (adrenergic fibers). The dispersed state is induced through either nerve fibers that probably discharge acetylcholine (cholinergic fibers) or through intermedine carried from the pituitary gland of the brain by the blood to the melanophores. If the pituitary gland is removed from a catfish, this fish can still darken but only partly (each melanophore can disperse its pigment to cover an area the diameter of which is at most about 100 microns). This reaction must depend exclusively upon cholinergic fibers (acetylcholine). When additional acetylcholine is injected into such a fish, the melanophore pigment is not further dispersed. This is true even when enough acetylcholine is injected to kill the fish. If into such a partly darkened fish a small amount of intermedine is injected, the fish will then fully darken. Intermedine, if injected into a pale fish, will also completely darken it. Hence acetylcholine as compared with intermedine is capable of inducing only a limited and well defined dispersion of pigment in catfish melanophores. The blanching agent adrenaline shows no such limitation in its action. It is noteworthy that acetylcholine in large doses is deadly to catfishes, but intermedine is not. What restricts the action of acetylcholine on the melanophores of this fish is not known. When under natural conditions a fish darkens, its melanophores are first excited through nerves (acetylcholine) and only subsequently does intermedine become an effective agent.

1. INTRODUCTION

WITHIN the last few years much that is new has been learned about the color changes in catfishes. It is now generally recognized that these changes are dependent almost exclusively upon melanophores which are of two kinds, micromelanophores in the epidermis, and macromelanophores in the derma. Of these the macromelanophores are the more efficient notwithstanding the fact that the layer in which the micromelanophores are located may become heavily impregnated with melanin particularly in fishes that have been for some time in the dark phase (Odiorne, 1937). It is also commonly

understood that the parts chiefly concerned with chromatic activation in *Ameiurus* are three: the pituitary gland, and two sets of nerves one dispersing and the other concentrating (Parker, 1934a). The pituitary gland acts on the melanophores through its product intermedine, carried in the blood and lymph from the gland to the color cells; the dispersing nerve-fibers are effective through their special neurohumor acetylcholine; and the concentrating fibers through adrenaline. These two sets of nerve-fibers have been classed in consequence of the neurohumors associated with them as cholinergic and adrenergic respectively (Parker, 1941).

Abramowitz (1936) appears to have been the first to point out that when two kinds of catfishes, one hypophysectomized and the other normal, are placed in a black-walled, illuminated vessel, the hypophysectomized individuals after adjustment of color are never so dark as the normal ones. This condition was independently noted by Veil (1937). But it remained for Osborn (1938) to show in a quantitative way what this limitation was. According to Osborn a normal catfish can disperse the pigment of its macromelanophores so that the color cells will cover areas the diameters of which average some 125 microns whereas a hypophysectomized individual can disperse this pigment only to some 70 microns. Osborn's statements were confirmed by Wykes (1938) on *Ameiurus* and by Enami (1939) on *Parasilurus*. Parker (1939a), who worked on *Ameiurus* as Osborn and Wykes had done, placed the diameter of the macromelanophores in a normal, fully dark catfish at some 145 microns and in a hypophysectomized one at about 100 microns. The differences between the estimates of Osborn and of Parker appear to be due to the fact that Osborn based his averages on small as well as on large macromelanophores whereas Parker measured only the larger and presumably mature color cells of this class. It is, however, perfectly evident from these several

records that hypophysectomized fishes fail to disperse their melanophore pigment as fully as normal fishes do. It is the aim of this paper to discuss the process of melanophore activation in *Ameiurus* as well as the limitations of the pigment activities in this fish.

2. MATERIALS

The fish used in this work was the common New England catfish *Ameiurus nebulosus*. For the sake of uniformity tests were restricted to specimens about 15 cm. in length. Such fishes weighed very closely to 50 grams each. When operations on living fishes were necessary the animals were first anesthetized by the convenient method of immersion in ice-cold water (Parker, 1939b). Much of the hypophysectomized material used in this work was prepared for me by Dr. L. H. Kleinholz to whom I wish to express my thanks. I am also under obligations to Mr. Frank White for the illustrative photographs.

The range of color change in the catfish is shown in Fig. 1 where individuals from the palest to the darkest are shown. Figs. 2 to 7 illustrate the states of the melanophores in three of the five stages seen in Fig. 1. The macromelanophores and micromelanophores of the palest stage are shown in Figs. 2 and 3 respectively. In both instances the pigment masses are approximately spherical, the diameter of the sphere in the macromelanophores being some 45 microns, that of the micromelanophores some 12 microns. The macromelanophores of the fully dark or coal-black stage are shown in Fig. 6, the micromelanophores in Fig. 7. The pigment in the macromelanophores of a coal-black fish covers incompletely an irregular area about 145 microns in diameter. The micromelanophores at this stage have irregular outlines with a few relatively long processes. These processes in many instances either anastomose or overlap in such a way as to appear to unite. A third and important color stage in the catfish is that seen in the middle fish in Fig. 1. This may be called the intermediate stage. At this stage the macromelanophores have short stubby branches (Fig. 4) and cover as a whole an area the diameter of which is roughly 100 microns or less. The micromelanophores of the intermediate stage (Fig. 5) are irregular in outline and possess relatively few rather delicate processes. These are apparently never in contact one with another.

3. HOW NEUROHUMORS ACT ON THE MELANOPHORES IN *AMEIURUS*

From the time of Spaeth's work on the color cells in fishes (1913) it has been customary to regard chromatophores the nerves of which have been severed as free from all forms of nervous control and in that sense independent. But it must be remembered that chromatophores in newly denervated areas of skin or in scales taken freshly from the fish's body still have attached to them more or less of the original nerve with its terminals. Agents which under these circumstances activate such color cells may do so either indirectly through the remnant of nerve still attached to the cell or directly by immediate contact with the protoplasm of the color cell itself. Thus this technique can yield no conclusive answer to the question of the indirect or direct action of such agents on color cells. This defect, which runs through almost all of the earlier work, was pointed out some years ago (Parker, 1934b) and it was then proposed to use in such investigations only those fishes which had been kept alive long enough after the severance of their chromatic nerves to insure the complete degeneration of these nerves. It was found by appropriate trials that ten to twelve days was ample time for this purpose. After the expiration of such a period no evidence of normal nervous activity could be discovered in the chromatic nerves and it was assumed that the necessary degree of degeneration had been reached. Chromatophores in such denervated areas were believed therefore to be completely free of all possible nervous associations. In inducing this degree of nerve degeneration it was found necessary to keep the fishes in water at about 20° C., for at the usual winter temperatures of 6° to 8° C. degenerative changes went on only very slowly or even not at all.

To prepare the melanophores in catfishes for tests with neurohumors the fishes were first hypophysectomized to rid them of their natural source of intermedine. Immediately after this operation two rather distantly related rays in their tails were cut whereby two caudal bands were produced. Such fishes were then set aside for from ten to twelve days to allow time for the disappearance of the last traces of intermedine from their blood and for the degeneration of the chromatic nerves in their caudal bands. The fishes were kept in an illuminated vessel the walls of which were of a grayish tint with the result

that each fish with its caudal bands assumed sooner or later an intermediate coloration. Once or twice during this preparatory period the incisions by which the caudal bands had been originally formed were recut to prevent the possibility of nerve regeneration. At the conclusion of this period it was assumed that the fishes were ready for neurohumoral tests in that they had lost all traces of intermedine and their caudal bands were devoid of active nerve-fibers. Catfishes in this state were then subjected to tests with the three neurohumors, adrenaline, intermedine, and acetylcholine.

The adrenaline used in these tests was the commercial preparation made by Parke, Davis and Company. It contained one part of adrenaline chloride in 1000 parts of fluid which in the main was physiological salt solution. In previous studies (Parker, 1940) of the action of adrenaline on the melanophores of *Ameiurus*, fishes of 50 grams weight were injected each with 0.2 cc. of this neurohumor at different strengths. The solutions varied from 1 part of adrenaline in 5000 parts of Ringer's solution to 1 part in 40,000,000 of the solvent. Solutions of 1 part of the neurohumor in 5000 parts of solvent to 1 part in 1,000,000 of solvent induced a general blanching of the whole catfish; 1 part of adrenaline in 5,000,000 or 10,000,000 parts of Ringer's solution caused a pale spot near the region of injection; and 1 part of adrenaline in 20,000,000 or 40,000,000 parts of solvent was without effect on the color of the fish. These figures agree fairly well with those given by Bray (1918) as well as the more recent ones by Pierce (1941).

In testing the way in which adrenaline acts on the melanophores by the catfish three hypophysectomized fishes with caudal bands prepared as already described were injected each with 0.2 cc. of adrenaline 1 part in 5000 of Ringer's solution. In 10 minutes the fishes had blanched fully though the caudal bands were not always as pale as the rest of the tail. In about an hour, however, the bands had become as fully pale as the rest of the fish and remained so for some two to three hours. In a second set of prepared catfishes an injection of 0.2 cc. of adrenaline, 1 part in 5000 of solvent, was followed in a quarter of an hour by moderate blanching of both bodies and bands which was intensified by a second injection of adrenaline. In these instances both bodies and bands blanched at essentially the same rate. Since the melanophores in these bands were fully devoid of nerve fragments and

yet responded to the adrenaline by concentrating their pigment it seems reasonable to conclude that this neurohumor acts directly on these color cells. This conclusion had already been reached in an earlier series of tests with this reagent on the color cells in the killifish *Fundulus* (Parker, 1934b).

The second neurohumor to be tried on the melanophores of the catfish was intermedine. This material was obtained by extracting with Ringer's solution the fresh pituitary glands of frogs or of catfishes or more conveniently by using Parke, Davis and Company's preparation of obstetrical pituitrine which contains intermedine as a byproduct. In the commercial manufacture of this preparation a small amount of chloretone is regularly added, a drug which is known to induce pigment dispersion in melanophores. However the amount present in this preparation, 0.5 per cent, was found to be quite ineffective in altering the states of the melanophores in *Ameiurus*.

Two catfishes of intermediate tint and prepared by hypophysectomy and caudal band formation were injected each with 0.2 cc. of obstetrical pituitrin (2 units) and allowed to remain for six hours in an illuminated vessel with gray walls. During this interval no color change either on the body of the fish or in its caudal bands was observed. Other catfishes prepared as those just described were injected with two doses each of 0.2 cc. pituitrin half an hour apart. These very regularly darkened slightly, the caudal band deepening in tint with the rest of the body. In some fishes a third and in others even a fourth dose of pituitrin was administered, whereupon the bodies of the fishes and their caudal bands often became very dark and in two instances the individuals were fully coal-black including their caudal bands. In other fishes two in number the dosage of pituitrin was double that just mentioned, namely 0.4 cc. per injection. These fishes also darkened and did so with this initial dose. In these instances as with the others the caudal bands and bodies darkened together.

An extract in Ringer's solution made from a single pituitary gland from a frog when injected into a prepared catfish profoundly darkened both body and caudal bands. The same was true of an extract of the pituitary gland of the catfish itself though this extract appeared to be less effective than that from the frog. Since in the presence of intermedine the melanophores of the caudal bands in prepared catfishes disperse their

pigment even to the maximum degree it seems fair to conclude that this neurohumor acts directly on these color cells without involving any special intermediate mechanism such as dispersing nerves.

The third and last neurohumor to be used in these tests was acetylcholine. This like intermedine is a darkening agent. It was used in the form of the commercial chloride. As is well known this agent is rapidly destroyed when injected into the animal body by the cholinesterase of the tissues. To prevent this destruction a preliminary dose of eserine is commonly given to the experimental animal, one part of eserine to 50,000 parts by weight of animal. At this concentration, however, eserine will darken a catfish more or less, but by reducing the amount to one part of eserine in 200,000 parts by weight of fish a concentration can be arrived at which will not darken the fish and will still protect the acetylcholine. This concentration was used in the following tests.

Into palish catfishes previously prepared by hypophysectomy, caudal band cutting, and subsequent injection with eserine, 0.2 cc. of solutions of acetylcholine of different concentrations from 1 part of the reagent in 100 parts of Ringer's solution to 1 part in 100,000,000,000 parts of solvent were injected. Nine different concentrations were used and all mildly darkened the catfishes except the weakest, 1 part of acetylcholine in 100,000,000,000 parts of Ringer's solution, which was without effect on the color of the fish. Three fishes in all received injections of this weakest solution and none of them showed signs of darkening. When two of these fishes were subsequently injected each with 0.2 cc. of acetylcholine 1 part in 100,000 of solvent they darkened moderately in half an hour showing that they were susceptible to the neurohumor. Concentrations of 1 part of acetylcholine in 100 parts of Ringer's solution to 1 part in 1000 of solvent not only darkened catfishes but led soon after to their death. The range of concentrations of acetylcholine within which this neurohumor was satisfactory for physiological tests was from 1 part in 10,000 to 1 part in 1,000,000,000.

The darkening that resulted from these various concentrations of acetylcholine made its appearance slowly and usually required from 20 minutes to half an hour to reach its complete development. It is a matter of interest to ascertain the relation of these physiologically effective concentrations to that found in the skin of a catfish

which had darkened normally. The concentration of acetylcholine in the skin of such a catfish has been estimated to be 1 part of the neurohumor by weight to 13,000,000 parts of skin (Parker, 1940). How is this concentration related to the range of the physiologically active concentrations that have just been given? When 0.2 cc. of a given concentration of acetylcholine is injected into a fish of 50 grams weight this neurohumor must be diluted thereby to 1/250 of its original strength. Consequently to produce in the fish as a whole, including its skin, a mixture of 1 part of acetylcholine in 13,000,000 parts of fish it would be necessary to use for injection a solution containing 1 part of acetylcholine in 52,000 parts of solvent. This concentration lies well between the physiological extremes already given for the catfish, namely, 1 part in 10,000 and 1 part in 1,000,000,000. That this concentration may well reproduce in the fish the state necessary to normal darkening is seen in the fact that when 0.2 cc. of such a solution are injected into a catfish of 50 grams weight the fish darkens in an entirely regular manner.

In the several tests with acetylcholine where the tails and caudal bands of pale, prepared catfishes were closely watched as they darkened, these two areas took on a deep tint together as was true when intermedine was similarly used. Hence it is concluded that acetylcholine like intermedine acts directly upon catfish melanophores and without the intervention of any additional elements. Thus all three of the neurohumors tested in this investigation, adrenaline, intermedine, and acetylcholine, appear to act directly upon the melanophores of the catfish in that their solutions activate a given color cell whenever there is mutual contact.

4. LIMITATIONS IN THE EFFECTS OF NEUROHUMORS

When 0.2 cc. of a solution of adrenaline, 1 part in 50,000, are injected into a catfish the whole fish irrespective of its original tint will blanch completely and under such circumstances the creature may well reach a maximum paleness (Fig. 1, extreme left specimen). Its macro- and micromelanophores will be found to be reduced to the spherical form (Figs. 2, 3). Thus adrenaline when fairly concentrated acts with complete efficiency throughout the whole range of melanophore response and induces full pigment concentration. When a weak solution of adrenaline, 1

part in 5,000,000 for instance, is injected subcutaneously into a catfish of intermediate tint, a pale area develops around the region of injection but this paleness does not spread far out over the skin. If the edge of this pale area is examined under the microscope, all transitions in melanophore states will be found there between those with fully concentrated pigment and those with pigment of an intermediate concentration. In other words this edge is not made up of a mixture of melanophores all of which have their pigment either fully concentrated or largely dispersed. This fact, that all intermediate degrees of spread of pigment are observable in this area, indicates that the "all or none law" appears to have no application to the activity of these melanophores. They seem to respond to varying degrees of stimulation and come to rest at any appropriate point. From this standpoint melanophores resemble smooth-muscle fibers (Spaeth, 1916).

In one respect the blanching of catfishes presents a slight anomaly. Many catfishes when they become pale in illuminated, white vessels fail to reach full paleness; they stop a little short of this end point. One of these is shown in the second fish from the left in Fig. 1. Under the microscope the melanophores in such a fish are not so nearly spherical as those shown in Figs. 2 and 3, but exhibit commonly slight protuberances, the roots of the pigmented processes. This state of incomplete blanching has already been recorded (Parker, 1940) and its common occurrence in hypophysectomized animals has led to the suspicion that in addition to adrenaline another concentrating neurohumor may be present in the catfish, one which can induce only incomplete blanching. I have, however, no conclusive evidence for such an agent. The identity of this possible activator with the W-substance of Hogben and Slome (1931) or the adrenaline-like material of Abramowitz (1936) is entirely hypothetical. When a partly blanched catfish such as has just been described is injected with an ordinary ample dose of adrenaline, it regularly blanches to complete paleness showing that its melanophores, though they came to rest at a stage somewhat short of full concentration, are capable of reaching this extreme if appropriately stimulated. The amount of adrenaline in the fish's skin at the semi-pale stage must therefore have been insufficient.

Intermedine, like adrenaline, can excite a full chromatic change, and in this instance from any

degree of paleness to full coal-blackness. This agent acts of course in the opposite direction to adrenaline. It has been intimated by some workers that the full coal-black state of the catfish can be induced only by the combined action of the two darkening agents intermedine and acetylcholine, but in my experience intermedine if applied in sufficient strength will of itself fully darken a catfish. Not all catfishes, however, show this reaction. Some stop short of full blackness, nor do they darken further on additional injections of intermedine or acetylcholine (Fig. 1, second fish from the right). Such individuals are incapable of becoming as dark as others, a peculiarity which is resident probably in their melanophores. Notwithstanding these apparent exceptions intermedine of itself appears to be capable of exciting pigment dispersion to a maximum degree in most catfishes.

Acetylcholine, the second darkening neurohumor, is remarkable for a limitation in its activity not seen in either adrenaline or intermedine. When properly protected by eserine acetylcholine can induce darkening in any blanched or partly blanched catfish to about an intermediate stage. In my own tests pale catfishes as already stated were made to darken till their macromelanophores covered an area some 100 microns in diameter. They failed entirely to reach a dispersion of 145 microns, the degree attained in coal-black fishes under the action of intermedine. The turning point for darkening with acetylcholine is a definite one and leaves the fish at a general color stage approximately intermediate (middle specimen in Fig. 1). The states of the macro- and micromelanophores in such a fish are reproduced in Figs. 4 and 5. The macromelanophores under these circumstances are characterized by short, blunt pigment processes and the micromelanophores by short, fine ones.

If into catfishes that have attained this degree of darkening from acetylcholine additional injections of this neurohumor are made, the fishes do not darken further but almost invariably die as they do when strong concentrations of this agent (1 part in 100 or in 1000 parts of solvent) are injected. Thus it appears that acetylcholine will darken catfishes only to an approximately intermediate point and when applied in larger amounts acts as a poison. It is interesting to note that of the three chief chromatic neurohumors in the catfish, acetylcholine is the only one that shows obvious poisonous properties.

It is further the only one that has associated with it a specific destructive agent, cholinesterase, that quickly removes it from the circulation of the fish. This complication may be interpreted from a biological standpoint as a protective measure in the economy of the fish.

When a catfish has been rendered as dark as it can be by acetylcholine an additional injection of intermedine will induce the animal to assume a much darker tint. In fact it may readily be brought by this means to the extreme coal-black stage. For reasons already given this subsequent response must be regarded as nothing more than the typical response to intermedine itself.

The discovery that hypophysectomy is followed by a limitation in the capacity for darkening in the catfish (Abramowitz, 1936; Veil, 1937) and that this limitation is a strikingly definite one (Osborn, 1938; Wykes, 1938; Enami, 1939; Parker, 1939a) is an interesting biological phenomenon. Why is it that acetylcholine will carry a melanophore from any condition of concentrated pigment to one of only half-dispersion and intermedine from any such state to full dispersion? The answer to this question is by no means obvious. However the solution is probably to be sought in some relation between the two neurohumors concerned and their direct action on the melanophore.

Immature melanophores in embryonic or larval animals are truly ameoboid cells. They creep about within the tissue spaces of the animal that gave rise to them and disperse and concentrate their pigment with striking and irregular change of form. As they mature they lose this protean capacity and in each successive dispersion they reproduce the form of the preceding one. This duplication of outline has been demonstrated by successive photographs of the chromatophores in crustaceans (Perkins, 1928; Brown, 1935). If, however, the photograph of a first dispersed phase is closely compared with that of a second one, as can be done in Perkins' figures (1928, Pl. 1), it will be seen that though the main pigmented branches and sub-branches agree in a remarkable way, the small terminal divisions do not do so. The cause of this terminal diversity is by no means clear. Is it possibly merely an out-of-focus effect in the photograph or may it be an incomplete dispersion of pigment at one phase as compared with the other? I regret to say that I cannot answer this question, particularly in relation to *Ameiurus* where the melanophores are so crowded as to

overlap and where therefore the outline of single color-cells cannot be followed as they can be in crustaceans (Fig. 6). After studying Perkins' figures with much care I am of opinion that there is a true diversity among the peripheral and terminal branches of the chromatophore repeatedly expanded as contrasted with the uniformity of its main branches. The larger branches are certainly rigidly constrained, but the smaller, peripheral and terminal twigs appear to retain the plasticity and freedom of movement that characterize whole embryonic color cells. If there should thus prove to be two different regions in the branches of catfish melanophores, one rigid and near the cell body and the other plastic and peripheral, might it not be that such regions are in some way related to the differences in melanophore responses to the two neurohumors concerned? Thus acetylcholine might be limited in its activation to the rigid part of the system whereas intermedine would not only disperse pigment over this portion but activate as well the distal plastic part of the branches. Such a suggestion is of course entirely hypothetical, but it may be helpful in leading to an experimental testing of the remarkable chromatic limitation shown by acetylcholine as contrasted with intermedine.

5. SUMMARY

1. The three chief chromatic neurohumors of the catfish, adrenaline, intermedine, and acetylcholine, all act on the melanophores of this fish directly.

2. Adrenaline, the probable neurohumor of the concentrating chromatic nerves in the catfish, can fully blanch this fish by inducing a complete concentration of its melanophore pigment.

3. Intermedine, a neurohumor from the pituitary gland of the catfish, can fully darken this fish by inducing a complete dispersion of its melanophore pigment.

4. Acetylcholine, the probable neurohumor of the dispersing chromatic nerves in the catfish, can darken a blanched fish to an intermediate dark tint but not further.

5. This limitation in acetylcholine as contrasted with intermedine may depend upon a limitation of its action to what appears to be a basal, rigid part of the melanophore system of branches as contrasted with a peripheral, plastic portion of this system. Both these portions may well be affected by intermedine.

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PLATE 1

All figures are photographic reproductions from the common catfish *Ameiurus nebulosus*.

FIG. 1. Five prepared catfishes showing the range of color change from full pale to coal-black. The coal-black specimen was eyeless; the other four fishes were normal.

FIGS. 2 TO 7. Photomicrographs of melanophores from preserved catfish tails. All figures are of the same magnification, approximately 110 diameters.

FIGS. 2 AND 3. Melanophores from the palest fish, extreme left, in Fig. 1. Pigment fully concentrated.

FIG. 2. Macromelanophores, average diameter about 45 microns.

FIG. 3. Micromelanophores, average diameter about 12 microns, with a few macromelanophores out of focus.

FIGS. 4 AND 5. Melanophores from the intermediate fish, middle one, in Fig. 1.

FIG. 4. Macromelanophores, covering areas with an average diameter of about 100 microns.

FIG. 5. Micromelanophores; outlines irregular and with scanty, fine processes.

FIGS. 6 AND 7. Melanophores from the coal-black fish, extreme right, in Fig. 1. Pigment fully dispersed.

FIG. 6. Macromelanophores, covering areas with an average diameter of about 145 microns.

FIG. 7. Micromelanophores, processes of different cells appear here and there to form a network.

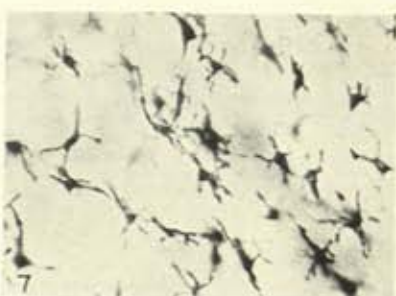
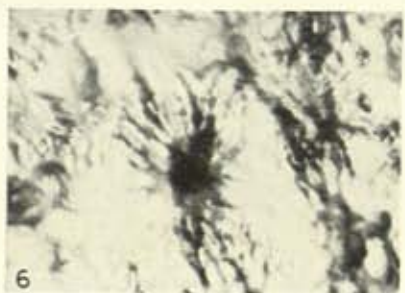
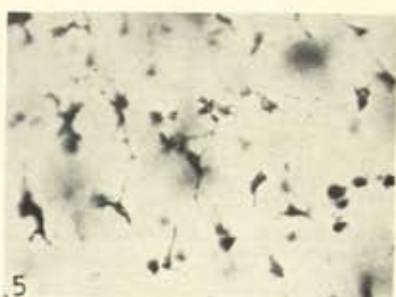
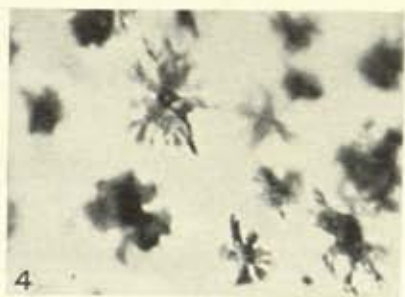
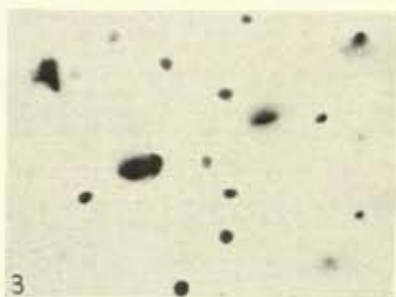
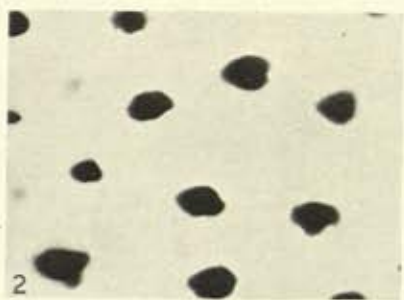
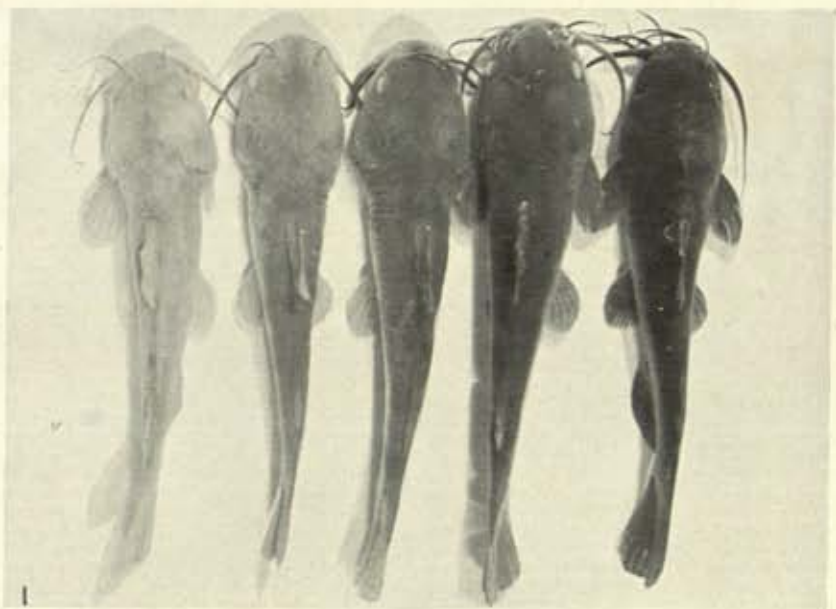
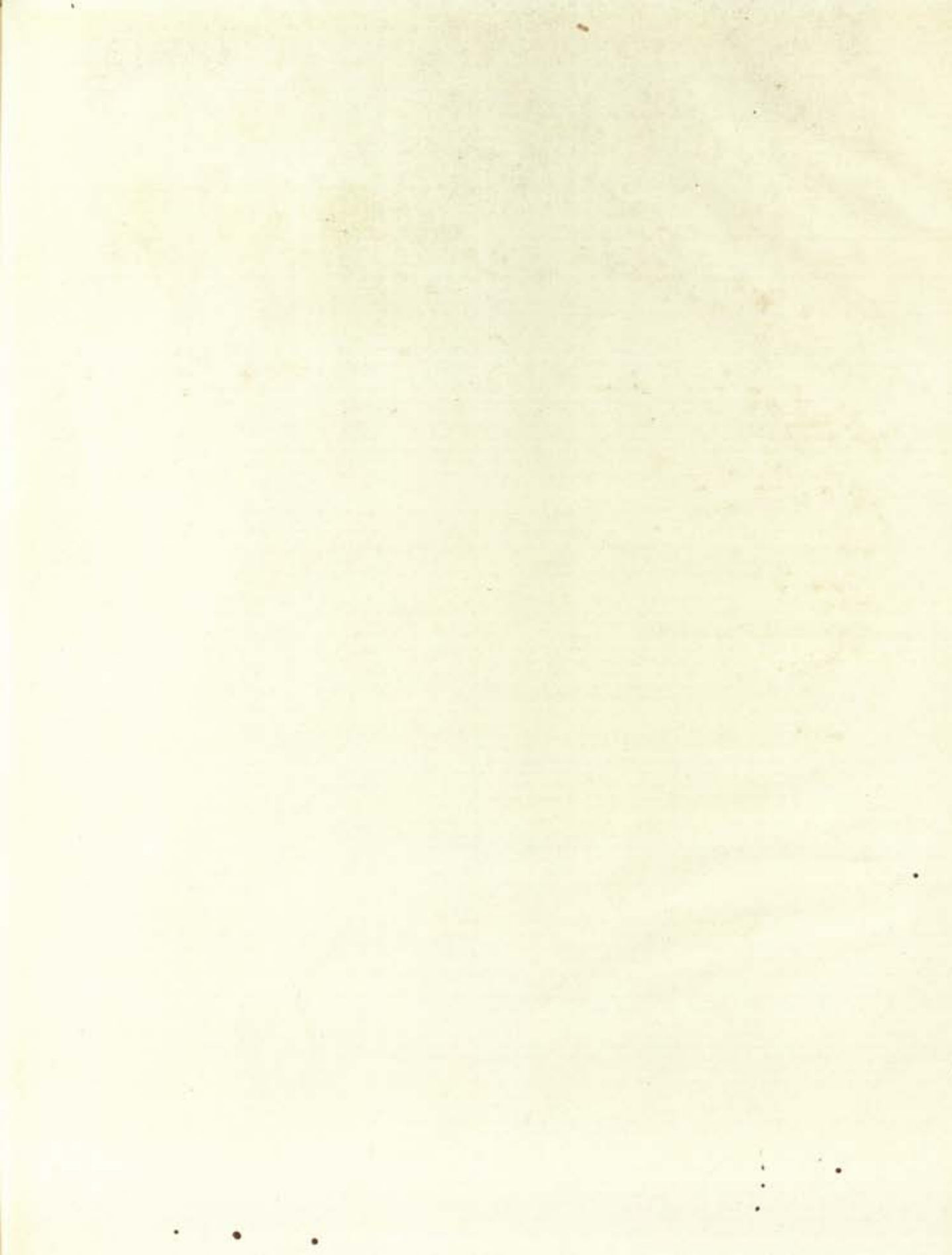


PLATE 1



GENETICS OF PARAMECIUM BURSARIA. II

SELF-DIFFERENTIATION AND SELF-FERTILIZATION OF CLONES¹

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ABSTRACT

Originally all members of a clone are of the same mating type; hence they do not conjugate together. At very long intervals (about 2,000 culture days), a clone may undergo self-differentiation into two mating types, which then conjugate (self-fertilization of the clone). In any clone self-differentiation yields in all cases the same two mating types, one of which is the original type of the clone. Different clones, even originally of the same mating type, may yield different sets of two types, so that the combination of two types produced by any clone is characteristic for it. In Variety I, with four mating types A, B, C, and D, all the six possible combinations have been observed: AB, AC, AD, BC, BD and CD. The two mating types produced by self-differentiation of a clone may each by renewed self-differentiation produce again the same two types.

The two clones produced from one by self-differentiation differ from each other in (1) mating type; they may also differ (2) in size and form of the individuals; (3) in rate of fission; (4) in readiness to conjugate. The population collected from a given locality often (but not always) consists of just two types, either of which may by self-differentiation produce the other.

By conjugation of the two mating types resulting from clonal self-differentiation, additional mating types are produced. In Variety I, a clone of type D has been observed to produce thus all the four types (A, B, C, D). Clones of type A, B, or C have each produced under observation three of the four types of the variety.

A considerable proportion of the pairs produced by self-fertilization die without reproducing, and this proportion increases as self-fertilization is repeated one or more times.

Through self-differentiation and self-fertilization the sexual reactions of a clone culture may become changed in a number of different ways.

In the first of these contributions and in other papers by the present author (1938, 1939, 1939a, 1940) it was shown that, in any variety, the individuals or clones of *Paramecium bursaria* belong to a number of different "mating types" which play in the mating behavior the role of diverse sexes. So far as fertilization is concerned the individuals or clones may be looked upon as hermaphroditic: each plays in conjugation the

role of both male and female. Each furnishes a migratory pronucleus which passes into the opposite conjugant, corresponding thus to the male germ cell. And each furnishes a stationary pronucleus which receives and unites with the migratory pronucleus, corresponding thus with the female germ cell. And each ex-conjugant continues to reproduce after conjugation has occurred. Fertilization is thus reciprocal. Nevertheless the individuals which conjugate together are physiologically differentiated into diverse mating types which play in the mating behavior the role of diverse sexes. Individuals or clones of the same mating type do not conjugate together; but those of different mating types may and do unite in conjugation.

The species was further shown in previous contributions to include three genetically isolated varieties, members of any one variety not conjugating with members of either of the other two varieties. In Variety I there are four mating types, designated respectively as A, B, C and D. In Variety II there are eight mating types, E, F, G, H, J, K, L, M. In Variety III there are again four, designated N, O, P and Q.

In earlier papers the three varieties have been spoken of as three "groups." As the three appear to be clearly separable, it seems best to use henceforth the designation varieties.

The different types and varieties, it may be remarked, are, in the present state of knowledge, not definable by fixed morphological or physiological characteristics apart from conjugation, but only by the system of inter-conjugation. The types and varieties can be identified with those here designated only by comparing their mating reactions with those of certain cultures now existing in the author's laboratory. Here are preserved living cultures of each of the sixteen mating types that constitute the three varieties. These existing cultures of the different types may be called testers.

To determine the variety to which an unknown clone belongs, its members must be tested suc-

¹This work was aided by grants from the Carnegie Corporation. To my assistants, Dr. Elizabeth Kirkwood and Mrs. Pauline Opitz, I am indebted for carrying out much of the detailed work.

cessively with testers of at least two of the mating types of each of the three varieties, until some type is found with which the unknown clone conjugates. The latter is thereby shown to belong to the same variety as the tester with which it conjugates. To determine next the mating type to which the unknown clone belongs, its members must be tested successively with testers of each of the mating types of that variety. If for example the unknown clone belongs to Variety I, some of its members must be mingled (separately) with each of the four testers of mating types A, B, C and D. Invariably (if it is mature) it is found to conjugate with three of the types but not with the fourth. This type with which it does not conjugate is the mating type to which it belongs (since individuals of the same type do not conjugate together). If the unknown clone is immature, the variety and type to which it belongs cannot be determined until it has become mature.

Except at certain rare periods, to be described, all members of a clone (derived by fission from a single parent individual) belong to the same mating type, so that members of the same clone do not conjugate together. The mating type is thus in ordinary fission inherited without change. For these relations, therefore, *the clone is the unit of observation and discussion*. All its individual members belong to the same mating type, so that one clone of Group I is of the type A, other clones are of the type B, others of C or D. For brevity, therefore, two clones will be spoken of as conjugating together; this means of course that the individual members of the two clones conjugate when they come in contact.

SELF-FERTILIZATION OF CLONES

Although members of the same clone do not ordinarily conjugate together, very rarely conjugation is found to occur among members of a single clone, so that the clone is self-fertilized. This self-fertilization of clones forms the subject of the present contribution. It has important consequences for the genetics and general biology of the organisms, and the processes accompanying it throw much light on the genetic constitution of the animals.

FREQUENCY OF SELF-FERTILIZATION; PROPORTION OF THE STOCK THAT UNDERGOES IT

Self-fertilization of clones is evidenced by the appearance of conjugating pairs in cultures con-

sisting of but a single clone. In *Paramecium bursaria* it occurs only at rare and seemingly irregular intervals. Usually when it occurs but a few pairs are to be seen among great numbers of nonconjugants. Many clone cultures may be kept under observation for long periods—for months or years—without any indication of self-fertilization. At unexpected times however pairs may be found in a clone culture, showing the occurrence of self-fertilization in the clone. Data are herewith presented to indicate the frequency (or infrequency) of its occurrence:

(1) From the population *He* (Variety I), collected April 21, 1938, twelve clones were cultivated, from twelve isolated individuals. These were kept under daily observation for more than a month. During the period of observation self-fertilization occurred in but one of the twelve (clone He6).

(2) From the population *Br*, 103 clones of Variety I were isolated November 18, 1939. These were kept under daily observation throughout the rest of November, all of December, and a part of January, 1940, somewhat more than six weeks. During this period self-fertilization occurred in but one of them—the clone Br48.

(3) From the population *DM* sixty clones were isolated December 24, 1939. These were kept under daily observation for one month. During this period, a single pair was found in the clone DM13, six pairs in the clone DM42. In the other 58 clones self-fertilization did not occur.

(4) From the population *San*, seventy-two clones were isolated December 24, 1939: of these, 71 belonged to Variety II, while one belonged to Variety I. The cultures of these clones were kept under daily observation from January 9 to February 14, 1940, a period of 36 days. Self-fertilization did not occur in any of them during this period.

(5) On August 2, 1940, 38 clones of Variety II were placed each in a Syracuse dish culture. These 38 clone cultures were kept under daily observation until October 20, a period of 79 days. During this period self-fertilization occurred in but one of the clones (clone S, of mating type J).

(6) From November 9, 1940, to January 14, 1941, a large number of cultures were kept under observation, examinations being made either every day or every alternate day. These were cultures in Syracuse dishes; they included 178 cultures of clones of Variety I, 224 of Variety II, and 63 of Variety III. Thus a total of 465

cultures were kept under observation for a period of 66 days. Among these certain clones were represented by several cultures, most of them by but one culture.

During the period of 66 days self-fertilization was detected by the presence of pairs in 15 of the 465 cultures. These 15 included 9 different clones.

From this last case some approximate idea may be obtained of the frequency of self-fertilization. There were 465 cultures observed throughout 66 days, making a total of 30,690 culture-days. During this time 15 of the cultures showed self-fertilization, or at the rate of one self-fertilization for 2,096 culture-days. This would be a rate of one self-fertilization per culture in 5.7 years.

When self-fertilization is detected by the presence of pairs in a clone culture, the proportional number of individuals undergoing self-fertilization varies greatly in different cases. In many cases but a single pair, or two or three pairs, are to be found in a culture containing many thousand individuals. From such a minimum the proportional number varies in different cultures up to cases in which a large majority of the individuals are undergoing clotting and pairing.

Furthermore, at times there occur epidemics of self-fertilization which continue in a given culture for several days or even weeks, with intervening periods in which no pairs are to be found. In such continuing epidemics the number of pairs to be found at any given time varies in different cultures from one or a few to very great numbers. The following specific cases will illustrate the varied conditions found:

(1) In a populous culture of the clone DM22 (Variety I) a single pair was found January 10, 1941. This clone had been under close observation from November 9, a period of two months, and was examined with care daily for 25 days after January 10, but no more pairs were found in it.

(2) A culture of the clone GM140a1 (Variety II) was kept under observation from November 9, 1940. No pairs were found until January 14, when a single pair was found and removed. Daily examinations showed no more pairs until January 21, when 13 pairs were found and removed. On the next day another pair was found. No more occurred, though daily examination was continued till February 3.

(3) The clone LP10 (Variety I) was represented by 6 cultures in Syracuse dishes. These were kept under observation from November 7, 1940, without the occurrence of pairs, till January 3, 1941, when six pairs were taken from culture 1. No pairs were present thereafter till January 6, when 2 pairs were found in the same culture, and removed. There were no more pairs till January 19, when 16 pairs were observed (and removed) in culture 1. On January 20 there were 3 pairs (removed); on January 22, 5 pairs (removed). All these were from culture 1: the other 5 cultures contained no pairs at any time. All were kept under daily observation until February 4, but no more pairs were found in cultures of this clone.

(4) In a culture of the clone 2H51a (Variety I) several pairs were observed and removed on each of the following days: January 5-6-8, 1940. On January 19, 20, 21 and 22 very numerous clots and pairs were present, so that conditions in the culture resembled those in mixtures of two populous clones of different type. Occasional pairs continued to be found until January 27; at this time the epidemic of conjugation was over.

No method has been discovered for producing self-conjugation of a clone at will. Apparently self-fertilization is to some extent favored by the conditions resulting from the following procedure. The clone is recultured by removing large numbers of its individuals to a new culture medium. Four or five days later the conditions seem favorable for self-fertilization, in case the clone is ripe for that operation. If some twenty-five clones are thus treated on a given day, it is possible that one or two of these will yield pairs in the course of the next four or five days. But even such a proportion is by no means always successful.

SELF-DIFFERENTIATION PRECEDING SELF-FERTILIZATION

All the members of a clone usually belong to the same mating type. When self-fertilization occurs, do the two individuals that unite in conjugation still belong to the same type, so that conjugation occurs between individuals of a single type? Or does there first occur a differentiation of the clone into two different types which then conjugate, as occurs in *Paramecium aurelia* (Kimball 1939, Sonneborn, 1939)? In the species just named there are but two mating types in any variety, while in *Paramecium bursaria*

there are four or eight, so that there are several different possibilities as to differentiation.

The answer to these questions is discovered by isolating the two members of "split pairs" and testing them. That is, before conjugation has been consummated the two individuals that were beginning conjugation are separated and isolated; then by appropriate tests the type of each is determined. This was practiced extensively in self-fertilizing clones of *Paramecium bursaria*. It reveals many important biological relations.

The delicate operation of isolating two individuals that are in the preliminary stages of conjugation is facilitated by special features of the process of clotting or agglutination which constitutes the first step in conjugation (see Jennings 1939, 1939a, for descriptions and figures of this clotting). At first two individuals merely adhere together slightly by any parts of the body surface that happen to come in contact. Often the anterior or posterior tip of one individual adheres to a tip or side of another, so that when one of the individuals moves, the other is pulled along with it. Before conjugation is finally consummated the two individuals must become placed side by side with oral surfaces in contact, a process requiring time (often an hour or more). But the early slight adhesion occurs only between individuals that can conjugate together, individuals that normally would conjugate together.

Two individuals thus lightly adhering in the early stages of conjugation are taken up with capillary pipette and removed to an isolated drop of fluid. In the process the two always become separated; they are then placed apart in different drops. The mating type to which each belongs is then determined by tests with individuals that are of known mating type.

The tests for determining the mating type of the two members of the split pair may be applied directly to the two individuals that were beginning conjugation. Or these two individuals may be cultured, each producing a numerous clone; then the tests may be applied to these clones. This latter method is much more convenient and gives the same results as the other. The general method of testing has already been described. Each member of the split pair must be tested with all the types of the variety to which it belongs. Thus, to determine the types to which the two members of a split pair belong, eight tests are required in case of Variety I, or Variety III, sixteen in case of Variety II.

Unfortunately for the convenience of study, self-fertilization occurs very rarely, and no means have been discovered for inducing it or hastening its occurrence. To investigate it therefore one is compelled to take advantage of such opportunities as present themselves spontaneously while one is cultivating and observing large numbers of cultures. Some hundreds of clone cultures were in progress at all times in our laboratory. The observations and experiments on self-fertilization herein set forth were made possible by this fact.

Self-Differentiation and Self-Fertilization in Variety I.—Self-fertilization was first examined by the aid of split pairs in a clone known as He6. Twelve clones were derived from the multiplication of 12 isolated individuals that were collected April 21, 1938; these twelve were designated He1 to He12. They were found by tests to belong to Variety I. On May 7, 1938, self-fertilization was found to be occurring in the clone He6, as shown by the presence of pairs. This clone was of the mating type D. Self-fertilization did not occur in the other eleven clones of He during the period of about a month during which they were examined daily.

To determine whether the clone He6 had before self-fertilization differentiated into different mating types, 18 split pairs were obtained in the way described above. The two members of each split pair are designated as *a* and *b* respectively—so that in each case *a* and *b* had begun to conjugate together. From each of the 36 members of the 18 split pairs (18*a* and 18*b*), a clone was obtained by allowing the individuals to multiply. The mating type of each clone was then determined by testing. In addition, the mating type of the two original individuals (*a* and *b*) of three of the pairs was determined directly.

The direct determination of the mating type for the single individuals *a* and *b* that have begun to conjugate is a delicate operation. For its successful performance, the individuals of the clone from which the split pairs are taken must differ in color from the individuals of the testers, so as to be distinguishable from the latter. This is not unusual; the clone from which the split pairs are taken may be much lighter green in color, in consequence of recent rapid multiplication, or in consequence of having been kept for some days in the dark. The required determination is made as follows. The individual *a* of the split pair is placed in a dense group of individuals of the type A. The individuals of type A either

adhere to the individual *a* or they do not. As soon as this is discovered, and before there is actual union between *a* and any individual of type A, the individual *a* is removed with fine pipette and tested in the same way in a dense group of individuals of type B. Next it is tested similarly with C, then with D. Three of the types attempt to unite with the individual *a*, while one does not; this latter is the type to which *a* belongs. A similar series of tests is made with the individual *b* of each pair.

In each of the three split pairs thus tested, one of the two members was found to be of the original type D, while the other was now of type A.

The 36 clones derived from *a* and *b* of the 18 split pairs were tested May 9 and 10, after each member (*a* and *b*) had produced a clone of many individuals. The tests were made as usual by mingling a part of the clone *a* with testers of A, other parts with testers of B, C and D. Tests with clone *b* of each split pair were made in the same way.

In every one of the 18 split pairs it was found by this method that the clone derived from one member of the pair was of the original mating type D, while the clone derived from the other member was of the mating type A. The six clones of the three pairs that were previously directly tested gave the same results as in the direct tests. That is, the clone derived from the single individual (*a* or *b*) of the split pair remains of the same type as its single ancestor. The mating type is inherited in vegetative descent from members of split pairs, just as in the usual vegetative reproduction.

The clone He6, therefore, originally of the mating type D, has before self-fertilization differentiated, some of its members transforming into type A. The two types D (original) and A (derived) then conjugate together.

Mating is thus between individuals of different mating type, even though all the individuals belong originally to the same clone (in this case the clone He6). Self-fertilization is preceded by self-differentiation into two types, an original type (D) and a derived type (A).

Self-Differentiation and Self-Fertilization in Variety II.—Somewhat more than a year later this matter was further examined in a clone of Variety II. In this variety there are eight mating types, as compared with four in Variety I.

Four clones were derived from four individuals collected in the Botanical Garden of the Johns

Hopkins University, August 20, 1939. These four were designated JH1, 2, 8 and 13. Within a week, and before they had been tested to determine the group and types to which they belonged, many pairs were found to be present in the clone culture of JH2, so that self-fertilization was occurring (August 27, 1939). The four clones were carried to California, and tests made September 14, 1939, showed that all belonged to Variety II. The clones of JH8 and JH13 were found to be of type E, the clone JH1 of type F. The clone of JH2, having undergone partial self-fertilization, no longer gave clear results as to the type to which it originally belonged.

On September 27, 1939, there were again pairs in clone JH2, so that it was again undergoing self-fertilization. Eighty-five split pairs were obtained and their two members isolated on that date. Clones were obtained by cultivating each of these, record being kept of each separately and of the pair to which it belonged. The clones of the different pairs were labeled S1*a*, S1*b*, S2*a*, S2*b*, and so on, up to S85*a* and S85*b*. The 170 clones were then tested with each of the 8 types of Variety II. In each of the 85 pairs one clone was of the type E, the other of type F. The clone JH2 had differentiated into these two types, which then conjugated. In this case it is not known to which of the two types the clone belonged at first.

On October 6, 1939, the clone derived from one member of the split pair S4 (above) was found to be undergoing self-fertilization. This clone, S4*a*, was of the mating type E. Six split pairs were obtained from it; and from the two members *a* and *b* of each, clones were cultivated. Tests showed that in each case one member of the pair was E, the other F. In addition, while this clone S4*a* was thus differentiating into two types, fifteen single free individuals were isolated from it (October 7, 1939), and from these, fifteen clones were obtained. Tests made October 16 and 17 showed that ten of these were of type E, while 5 were of type F.

In this case, therefore, the clone S4*a*, originally of type E, has partly transformed into type F; then in many cases the two have conjugated. Also single free individuals of each of the two types are present (October 7).

One of the clones of type F, derived from one of the single free individuals above mentioned, underwent self-fertilization October 16 and 17. From it 24 split pairs were obtained and clones were cultivated from the two members (*a* and *b*)

of each. In every one of the 24 one member was found by test to be of F, the other of E. In this case a clone that was originally of type F has at self-differentiation transformed partly into type E.

Thus clones that are originally E differentiate into E and F, as do also clones that were originally F. In each case the clone is seemingly of the constitution (EF); such a clone (EF) may manifest itself either as E, or, after transformation, as F. In the case described there has been a double transformation: a clone of type E (clone S4a) differentiated into E and F; then one of these F clones (produced from E) again differentiated into E and F. This double transformation is of much significance for the interpretation of the differentiation—a matter to be dealt with later.

In all the cases described above, it will be observed that every split pair from any clone consists of the same two types. The 18 split pairs from clone He6 each consisted of D and A. Of the 115 split pairs derived finally from the clone JH2 each consisted of E and F. Thus any

single split pair shows the two types into which any clone differentiates. This situation was found in all the cases in which self-fertilization occurred in a clone known not to have become differentiated beforehand, in consequence of an earlier self-fertilization (for the results of successive self-fertilizations see a later section).

Thus, to determine the type into which an existing uniform clone differentiates, large numbers of split pairs are not required. In some later studies, therefore, smaller numbers were employed, though usually six to twenty split pairs were examined.

In the course of the years 1938–1941, self fertilization was observed and analyzed by the use of split pairs in 32 clones, of which 15 were of Variety I, 17 of Variety II. Self-fertilization was observed also in two clones of Variety III, but these were not studied by means of split pairs.

In tables 1 and 2 the chief data on the self-fertilizing clones will be found summarized for varieties I and II respectively. The tables include at the left a list of the clones, next the dates

TABLE 1

SELF-DIFFERENTIATION AND SELF-FERTILIZATION OF CLONES IN *Paramecium bursaria*, VARIETY I

List of clones in which self-differentiation and self-fertilization were observed, with dates, number of split pairs examined, the original mating type (if known), and the two mating types resulting from differentiation.

Designation of Clone	Dates	Number of Split Pairs	Original Type	Mating Types Resulting
He6	May 4, '38	18	D	D and A
J17b1	Nov. 7–12, '39	60	B	B and D
2H58a	Nov. 11, '39	33		B and A
Br48	Nov. 29–Dec. 4, '39	13	B	B and C
2H34b	Dec. 1–14, '39	13		B and D
2H54b	Dec. 1–14, '39	22		B and D
2H51a	Jan. 5–11, '40	8	B	B and C
2H51a	Jan. 19–20, '40	18	B	B and C
2H51a	Jan. 21, '40	14	B	B and C
DM13	Jan. 31, '40	1	D	D and C
Lo1	Nov. 7, '40	6	D	D and C
Lo1	Nov. 12–15, '40	7	D	D and C
LP10	Jan. 3, '41	4	D	D and C
Wat 1-S6b	Jan. 13, '41	9	B	B and C
Wat 1-S13a	Jan. 17, '41	12		A and B
Lo12	Feb. 2, '41	19	C	C and B
Lo12-S21a	Feb. 27, '41	11	C	C and B
BD214	Mar. 4, 5, '41	11		A and D

Note: In the clones 2H58a, 2H34b and 2H54b the original type was practically certainly B. But tests were not made till after self-differentiation had occurred. In all cases, however, (1) the other ex-conjugant of the pair (2H58b, 2H34a, 2H54a) was B, and it is known that in 98 per cent of all cases the two ex-conjugants of a pair are the same in mating type; (2) after self-fertilization had begun a very large majority of the individuals of the clone were in each case of type B; these were presumably the individuals that had not differentiated. In clone BD214 tests had shown that the original type was not D. It must therefore have been A, though it is not so listed in the table because the proof that it was A is only indirect.

TABLE 2

SELF-DIFFERENTIATION AND SELF-FERTILIZATION OF CLONES IN *Paramecium bursaria*, VARIETY II

List of clones in which self-differentiation and self-fertilization were observed, with dates, number of split pairs examined, the original mating type (if known), and the two mating types resulting from differentiation.

Designation of Clone	Dates	Number of Split Pairs	Original Type	Mating Types Resulting
JH2	Sept. 27, '39	87		E and F
JH2-S4a	Oct. 7, '39	6	E	E and F
JH2-S4a1	Oct. 16-17, '39	24	F	F and E
Mo1	Nov. 28-Dec. 5, '39	16	F	F and M
Mo3	Nov. 28-Dec. 5, '39	10	M	M and F
Mo4	Dec. 4-7, '39	7	M	M and F
Mo2	Dec. 4-7, '39	3	F	F and M
NH13	June 27-July 6, '40	See note	H	H and E
S	July 6, '40	10	J	J and L
S	Aug. 15-16, '40	5	J	J and L
GM215a2	July 6, '40	3	K	K and F
Fd	Dec. 12-27	21	E	E and F
HV3	Dec. 2-Jan. 6, '40	15	F	F and G
HV3-S4b	Jan. 6, '40	10	G	G and F
Fl	Dec. 27, '40	1	G	G and F
GM140a1	Jan. 22, '40	1	H	H and K
Coq5	Feb. 27-March 1, '41	12	F	F and G
Coq5-S9a	March 12-13, '41	7		F and G

Note: In clone NH13, the types resulting from self-differentiation were determined, not from split pairs, but from the two types of individuals present in the culture while self-fertilization was occurring.

at which self-fertilization occurred, the number of split pairs tested in the manner described above, the mating type to which the clone belonged before self-differentiation, and in the last column the two mating types which resulted from self-differentiation (the original and the derived types).

Before taking up the general relations involved, certain special features of the tests may be mentioned.

At times, instead of a pair of individuals beginning conjugation (a "split pair"), a small clot of three or four individuals clinging together is taken from the self-fertilizing culture. Each of the three or four individuals is isolated, a clone obtained from it, and this is tested in the usual way. Invariably such a small clot contains individuals of just the two mating types that compose any split pair. Thus in the case of the self-fertilizing clone 2H51a of Table I the split pairs all consisted of one individual of type B and another of type C. In one case there was a clot of 3; in this two individuals were of type B, one of type C. Again, the clone S (Table 2) yielded at self-fertilization split pairs that consisted of the two types J and L. In four cases clots of three were investigated; in each case two of the individuals were of type J, one of type L. Such

relations were found in all the many cases of this kind that were examined.

A possible source of error in isolating two individuals that are in the preliminary stages of conjugation lies in the fact, described in earlier papers (1939, 1940) that often there is close and continued contact between two individuals that do not finally conjugate. In such association the two individuals in contact swim together in a coordinated way, but there is no physical cohesion between the two as there is between two individuals that will finally conjugate. With practice this enables the operator to distinguish between the two cases. In the preliminary stages of conjugation there is actual adhesion, so that the motion of the two individuals is often not coordinated. One pulls the other out of its normal course in consequence of the irregular adhesion. Only pairs in which this occurs are certainly in the preliminary stages of conjugation. Unless care is exercised, however, individuals that are merely swimming together in contact may be taken up in place of pairs that are actually adhering. This is more likely to occur in the common case that the culture contains very few adhering pairs, so that the investigator is anxious not to miss any of the possible cases. If two individuals, not adhering,

but merely in contact, are taken up and isolated, it is found upon test that they both belong to the same mating type; we are then not dealing with a genuine "split pair". In practice such cases are rare; they have occurred but a few times among the hundreds of split pairs that have been examined.

Very old clones in which self-fertilization has occurred long ago, so that the descendants of the pairs formed have become mature, give results which are diverse from those presented in Tables 1 and 2. Such cases are described later.

In Table 1, of Variety I, it may be observed that in none of the clones listed was the original mating type certainly A, and from this the inference might be drawn that type A does not undergo self-differentiation and self-fertilization. However, self-fertilization had been observed in two clones of mating type A (namely clones *l* and 88a1) before the method of analysis by means of split pairs had been devised. Also it is practically certain, on indirect evidence, that in clone BD214 of Table 1 the original type was A.

GENERAL RELATIONS IN SELF-DIFFERENTIATION

We shall take up the general relations in self-differentiation as illustrated by the cases summarized in Tables 1 and 2, giving such additional facts as are pertinent.

1. In all the cases analyzed by the use of split pairs, it was found that self-differentiation of the clone had occurred before self-fertilization. All members of the clone are originally of a single mating type. At a certain period part of its members transform into a second or derived mating type; then individuals of the two types agglutinate and conjugate. Conjugation is thus, in all cases observed, between individuals of different mating type.

What is the nature of the process by which self-differentiation into two types occurs? It seems probable that some nuclear change underlies the differentiation. In *Paramecium aurelia* such a change of type is produced at endomixis. In *Paramecium bursaria* endomixis occurs very infrequently (Erdmann 1927) and seemingly not at regular intervals. This is likewise the case with self-differentiation and self-fertilization. One is led to suspect, therefore, that endomixis or some similar nuclear change occurs at the time of self-differentiation. A cytological investigation is obviously needed. The phenomena present

great difficulty, since self-differentiation is very infrequent, and is not outwardly manifested. Moreover, it is possible that there is a period of immaturity following self-differentiation, so that when self-fertilization is discovered through the presence of pairs in the clone culture, the nuclear processes of self-fertilization may have been long completed. The conjugation which follows self-differentiation of course includes complex nuclear changes which would make detection of the nuclear changes peculiar to self-differentiation very difficult, in case the two are occurring at the same time in the clone culture.

2. An important feature of self-differentiation appears in Tables 1 and 2. In any culture of a particular clone, self-differentiation yields in all cases the same two types (rare apparent exceptions appear in old clones in which self-differentiation has occurred long before the split pairs are obtained, but such are not real exceptions, as explained later).

In *Paramecium bursaria*, as before mentioned, there are more than two mating types. In Variety I there are four, in Variety II there are eight. A particular two out of these four or eight result from the self-differentiation of any clone culture. In clone He6 the two types produced are always D and A, never either types B or C. The original type of this clone is D: self-differentiation adds to it the derived type A. In the clone of JH2 of Variety II self-differentiation yields in all cases the two types E and F, never any of the other six types (G to M). A culture that is first of type E produces only the additional derived type F, while a culture that is at first of type F produces only the additional derived type E. Similar relations hold for all the cases of self-differentiation analyzed and summarized in Tables 1 and 2.

3. Do all clones of a certain original type, as D, produce at self-differentiation a particular derived type, as A (as in clone He6 above)? In other words, are two particular types always associated together in the constitution of a clone, as D and A are in the constitution of the clone He6, or as E and F are in the constitution of the clone JH2?

These questions are answered in the negative by the data of Tables 1 and 2. Table 1 contains several cases of self-differentiation in clones that were originally of mating type D. The first of these listed (He6) gave rise at differentiation to the derived type A, while several others produced type C. In some cases in which the original type

is uncertain, the two types D and B are associated as the products of differentiation. Again self-differentiation was observed in six clones that were originally of type B. Of these five produced the derived type C, while one produced the derived type D. In another case (clone 2H58a) B and A were the products of differentiation.

In Variety II (Table 2) self-differentiation was observed in five clones that were originally the mating type F. Two of these produced at self-differentiation the derived type M, one produced type E and two produced type G. Two clones were originally H; one differentiated into H and E, the other into H and K.

It is clear, therefore, that different clones originally of the same mating type may and do at self-differentiation give origin to different derived types.

4. Thus any particular clone is so constituted as to yield at self-differentiation a particular combination of two mating types, different clones being diverse in the combinations which they produce. The combination produced by any clone is characteristic for that clone. The constitution of the clone may be designated by the pair of types that it produces. The clone He6 was of the constitution (DA): it could manifest itself either as mating type D or as A. Using this notation, we have in Table 1 and 2 clones of the following constitutions:

Variety I: (AB), (AC), (AD), (BC),
(BD), (CD).

Variety II: (EF), (EH), (FG), (FK),
(FL), (FM), (HK), (JL).

Thus in Variety I all the six possible combinations of two types have been found to occur. In Variety II, of the 28 possible combinations of two types from eight, eight have thus far been found. It seems probable that in Variety II, as in Variety I, all the possible combinations of two types may ultimately be found to occur.

5. When a given clone undergoes self-differentiation at successive periods or when in a single clone self-differentiation occurs in two or more different cultures, in each case the same two types are produced.

Thus the clone JH2 underwent self-differentiation at three successive periods: September 27, October 6 and October 17, 1939. At each of these periods, it gave rise to the same pair of types, E and F. Similarly the clone S underwent self-differentiation July 6 and again August 15, 1940. It produced in both cases the same

two types J and L. The clone 2H51a differentiated January 6 to 8 and January 19 to 21, 1940. In both periods it gave rise to the two types B and C.

In some observed cases self-fertilization in a particular clone occurred in two different cultures which had been cultivated separately for a considerable time. Such are the following:

Clone S, of type J, Variety II. This clone existed in a number of cultures. On July 6, 1940, pairs were present in one of these; on August 15 to 16, pairs were present in another. The two cultures had been cultivated separately for more than six weeks, probably for much more. Split pairs from both consisted of the same two types, J and L.

Clone Fd, of type E, Variety II. December 12-14, 1940, there were pairs in two cultures which had been cultivated separately since May 4, 1940; that is, for 7 months and 8 days. Split pairs showed that the two differentiated into the same pair of types, namely E and F.

Thus a given clone retains its constitution (as to mating type) certainly for long periods, so that when it differentiates it produces throughout the same two types. Clone JH2 yields in all observed cases types E and F; clone Fd also yields E and F. Clone S yields J and L, clone 2H51a yields B and C, and so on.

6. After a clone has by self-differentiation produced two mating types, each of these may later by renewed self-differentiation again produce the same two mating types. This is exemplified in clones JH2 and HV3 (Variety II) in Table 2. The clone JH2 produced at self-differentiation the two mating types E and F. Clones of each of these types so derived later again differentiated, each producing anew the types E and F. The clone HV3 was originally of the mating type F. At self-differentiation it produced the derived type G, and a clone of this type (designated HV3-S4b) by renewed differentiation produced the original type F. Thus after self-differentiation of a clone, each of the two types produced may still produce the other.

The fact that a clone of given mating type may by self-differentiation produce a particular additional mating type presumably rests upon the fact that these organisms are diploid in their chromosomal constitution. After self-differentiation the two clones produced must be still diploid, since each can still produce two different

mating types. This is consistent with the cytological processes that occur in endomixis. Endomixis includes a division of the micronucleus, presumably reductional. Then, according to the recent work of Diller (1936) there is a union of two of these reduced nuclei, to form anew a diploid nucleus ("autogamy"). The occurrence of autogamy at endomixis is confirmed genetically by the observations of Sonneborn (1939) in *Paramecium aurelia*. The two types resulting from endomixis are consequently diploid, as was the parent clone before self-differentiation.

Self-differentiation might conceivably occur in two different ways. (1) On the one hand a single individual might through endomixis produce both the types that result from self-differentiation. The two types would then presumably separate at a fission occurring immediately after endomixis; this is what occurs in *Paramecium aurelia* (Sonneborn 1937). (2) Or single individuals of the original type might transform at endomixis into the derived type, leaving other individuals of the original type unaltered. In this second case the "original" and "derived" types would differ in the time that had elapsed since a differentiation had occurred; it might then be expected that the original type would differentiate anew earlier than would the derived type.

This appears to be actually the case in *Paramecium bursaria*. After self-differentiation has occurred, the clone derived from the original type (obtained from split pairs) is very frequently observed to undergo again self-differentiation, while the clones from the derived type very rarely do so. Among all the cases recorded in Tables 1 and 2, renewed self-differentiation in the clone of derived type was observed but twice, in the clones of JH2 and HV3, of Variety II. Renewed self-differentiation in the clones of the original types was on the other hand observed many times.

7. After self-differentiation of clones into morphologically and physiologically diverse types, the two types into which a clone differentiates are of course physiologically different, in the very fact that they are diverse mating types. The clone He6, originally of type D, produces the derived type A, which reacts in conjugation in a different way from D.

Do other differences, physiological or morphological accompany the physiological diversity of mating type? Evidence on this point gradually accumulated, as follows:

Differences in Size and Form.—It was frequently noticed that in the pairs formed in the process of self-fertilization, one of the two united individuals is larger than the other. This was at first thought to be a transitory phenomenon, without further significance. But some attention was given to it, at first in a rather loose way; later when it was found to be significant it was examined with care.

On November 11, 1939, the clone 2H58a, almost certainly of type B, underwent self-fertilization. Thirty-three split pairs were obtained. In most cases one of the adhering individuals appeared to be smaller than the other. Where this was true the larger member of the split pair was in a routine way placed in the left-hand depression of the slide and designated *a*, the smaller being transferred to the right-hand depression and designated *b*. From each of the 66 individuals of the 33 split pairs (33*a* and 33*b*) a clone was obtained, and when the 66 clones had sufficiently multiplied, each was tested to determine the mating type. Of the 33 *a*'s (larger), 30 were of the original mating type B; of the 33 *b*'s (smaller), 30 were of the derived type A. In only three pairs were the relations reversed; *a* was of the derived type A, while *b* was of the original type B. In these three exceptional cases presumably the difference in size (if any) was so slight that they were not correctly classified.

Thus in this clone at the time of conjugation the individuals of the original type B were larger (in the great majority of cases, at least) than those of the derived type A. Not only this, but in the clones derived by fission from the split pairs it was noticed, to my surprise, that the differences in size persisted; they were inherited in vegetative reproduction.

This led to a more exact study of the matter in some later cases of self-fertilization. The clone 2H51a, of mating type B, underwent self-fertilization during a considerable period beginning January 5, 1940. From this clone 40 split pairs were obtained. In each pair one member was of the original type B, the other of the derived type C.

Eighteen of these split pairs were obtained January 20, 1940. Opportunity was then taken to make a more exact study of differences in size and form, and their significance. It was observed that in all of the 18 pairs one member was slightly longer and more slender, the other shorter and relatively thicker. The long slender

member was in each case designated *a*, the short thick one *b*. From each of the 36 individuals a clone was derived, and the members of the clones showed the same morphological characteristics as the individuals from which they were derived. The members of all the eighteen *a* clones were long and slender; the members of the eighteen *b* clones were short and thicker. Later the thirty-six clones were tested for determination of the mating type. In every case the *a* clone, of long slender individuals, was of the original type B; while the *b* clone, of shorter thicker individuals, was of the derived type C.

Eight other split pairs from the same source had been obtained earlier (January 6 to 8) and clones derived from them were in existence, but had not been tested. It was decided to try whether it would be possible by means of the differences in size and form to classify these correctly into the two mating types B and C. In each of the eight the clone from one member of the pair consisted of individuals that were long and slender, and therefore presumably of type B. The clone from the other member consisted of shorter thicker individuals; these clones were presumably of the derived type C.

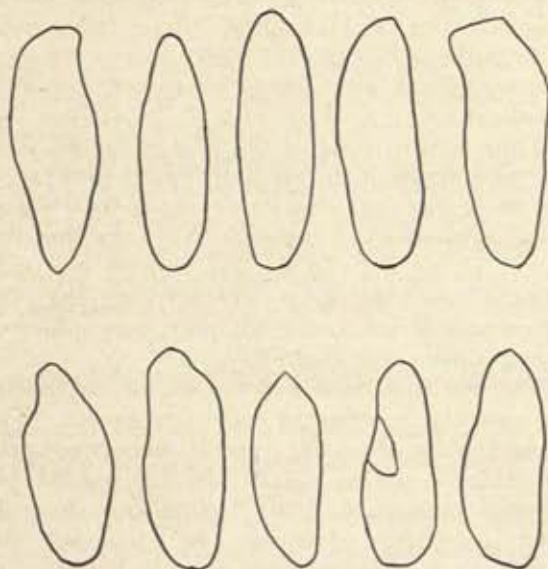


FIG. 1. *Paramecium bursaria*. Camera outlines of typical specimens resulting from self-differentiation of the clone 2H51a; all drawn to the same scale. The upper row shows typical individuals of the original mating type B (larger, more slender); the lower row typical individuals of the derived mating type C (smaller and proportionately thicker). From two clones derived from the two members of a split pair isolated January 8, 1940 and cultivated separately till February 6, 1941, on which date they were fixed and drawn. Magnification, 288 diameters.

Later tests confirmed these attributions. In the two sets together there were 52 clones descended from the two differing members of the 26 pairs. In every pair the clone of long slender individuals was of the original type B, while the clone of shorter thicker individuals was of the derived type C.

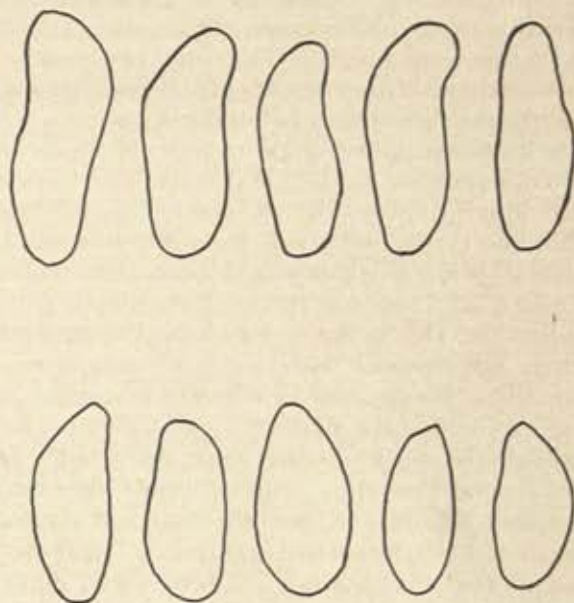


FIG. 2. *Paramecium bursaria*. Camera outlines of typical specimens resulting from self-differentiation of the clone 2H54b; all drawn to the same scale. The upper row shows typical individuals of the original mating type B (larger, more slender), the lower row typical individuals of the derived mating type D (smaller and thicker). From two clones derived from two members of split pairs isolated December 10, 1939, and cultivated separately till February 7, 1941, on which date they were fixed and drawn. Magnification, 288 diameters.

These differences (in possibly slightly less marked form) continued to be characteristic for the clones of the two different types for more than a year. Fig. 1 shows in juxtaposition camera outlines (at the same magnification) of characteristic groups of individuals from B and C clones derived from a split pair (Number 9) of this stock; as they were on February 6, 1941; more than a year after the clones were isolated.

Split pairs obtained from the clone 2H54b (December 1 to 14, 1939) showed the same sort of differences between the two members. In this case the original type was probably B, the derived type D. The individuals of the clones of the original type B were long and slender; those of clones of the derived type D were short and thick. These differences still persist more than

thirteen months after the clones were originated from the two members of split pairs. This is shown in Fig. 2. Here are camera outlines, at the same magnification, of characteristic individuals of the two types, on February 7, 1941.

Fig. 3 shows further a set of pairs from this clone 2H54b, showing the difference in size. In each case the larger member is of the original type B, the smaller member of the derived type D. These pairs were obtained February 7, 1941, by mixing members of clones from split pairs obtained December 10, 1939.

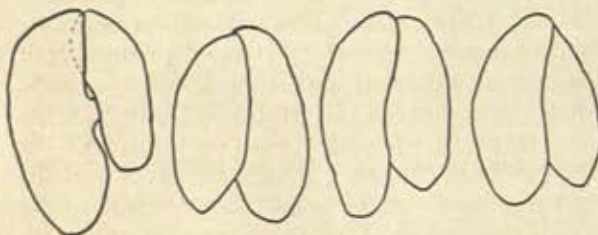


FIG. 3. Camera outlines of a number of pairs from self-fertilization in clone 2H54b, showing the difference in size of the two members. In each pair the larger member is of the original mating type B, the smaller one of the derived mating type D. Pairs obtained February 7, 1941, by placing together clones derived from two members of split pairs isolated December 12, 1939 and cultivated separately till February 6, 1941. Magnification, 288 diameters.

In the above described clones of Variety I, therefore, self-differentiation of the clone produces two types that differ not only physiologically, as to mating type, but morphologically, as to size and form. Those that remain of the original type (B in the cases above described) are longer and more slender than those that have been transformed into the derived type (A, C or D in the three different clones described). These differences are perpetuated in vegetative reproduction, so that they still persist in the clones derived from the individuals of the split pairs.

Variety II was less studied from this point of view. But in a clone S of this variety there were indications of a difference in size between the two types produced at self-differentiation. In this case, however, it was the derived type which had the larger individuals. The clone S was originally of type J; it produced at self-differentiation the additional type L. In six split pairs taken August 15 to 16, 1940, there was a marked difference in size between the two members. The larger member was designated *a*,

the smaller *b*. One of the split pairs was lost; in the remaining, five tests showed that the larger member *a* was in each case of type L, the smaller member *b* of type J.

But persistent differences in size and form are not to be observed in all cases of self-differentiation, though they appear to be common. In many cases it is not possible to classify accurately by size or form into two mating types before tests are made. The differences in size and form are either absent or so slight as to be readily masked by differences due to other causes. The difference in size commonly observed between the two members of split pairs appears in many cases to disappear in the growth and multiplication that produces the later clones. The same clone may at one date yield split pairs that uniformly differ in size and form of the two members, in correspondence with the mating types to which they belong; at another date produce split pairs that do not show this uniform diversity. So in the clone 2H51a, described above, 26 split pairs showed striking and uniform differences between the two mating types, but 14 other split pairs obtained from this clone at a later date (January 21) had these differences much less clearly defined. An attempt to distinguish beforehand in 12 of these the two mating types was successful in only nine cases out of the twelve.

The differences in size and form, where they exist, seem to be indices of a constitutional difference, but this constitutional difference does not always manifest itself in this particular way.

Differences in Fission Rate.—Besides the morphological differences there were in the case of the two types produced by self-differentiation in the above clone 2H51a differences in fission rate. The clones from the two members (*a* and *b*) of any pair were kept side by side in small watch glasses. As set forth above, in every case the clone from one member of the pair consisted of individuals that were longer and more slender, and were of mating type B, while the clone from the other member was shorter and thicker and was of mating type C. On January 20 it was observed that in each pair of cultures, one of the two swarmed with individuals, while in the other the individuals were few. The difference was very great. Further examination showed that in every case it was the clone of longer slender individuals of type B that had multiplied greatly, while the clones of C type (short and thick individuals) had multiplied very little. In this case, therefore, the original type B multiplied more

vigorously than the derived type C. A similar difference was observed in the clones from split pairs of certain other clones in Variety I.

In the self-differentiation of clone S of Variety II, again it was the derived type L that multiplied more rapidly than the original type J. Ten split pairs were obtained July 6, 1940, *a* and *b* of each being allowed to multiply separately; later (as before noted) one of each pair was found by test to be of type J, the other of type L. On July 9, after three days, the number of individuals present was counted for each *a* and *b* clone separately. In every case the number was much greater in the clone which later tests showed to be L. The numbers present in the two clones from each of the ten pairs were as follows:

J clones: 8-8-5-4-6-7-5-11-4-10.

Mean: 6.8.

L clones: 15-17-27-28-10-17-16-27-16-16.

Mean: 13.9.

In the J clones the range of variation is from 4 to 11; in the L clones from 10 to 28. The mean is nearly three times as great for the L clones as for the J clones. In this case, therefore, the clones of the derived type (L) had at first a more rapid fission rate than those of the original type (J).

In clone NH13 of Variety II there is again more rapid fission in the clones of the derived type (E), as compared with those of the original type (H). Five days after isolation of twelve clones, four of which turned out to be H while eight were E, the numbers present in the H clones ranged from 16 to 32, with a mean of 21; while the numbers present in the E clones ranged from 44 to 72, with a mean of 58.

But as in the case of size differences, a uniform difference in fission rate in favor of one of the types is by no means always found in self-differentiation. In many cases the slight variations in rate seem distributed indiscriminately in the two types.

Differences in Readiness to Mate.—In a considerable number of cases there is a marked difference between the two types that result from self-differentiation, with respect to readiness to accomplish the mating reaction. In testing the clones to determine the mating type, members of each clone (*a* and *b* in the case of split pairs) are mingled separately with testers of each of the four (or eight) mating types of the variety. Frequently there is with all but one of these tester types an immediate reaction; clots of adhering

individuals are formed from which united pairs later emerge. (The type with which reaction does *not* occur is of course the type to which the tested clone belongs.) But in some tested clones this reaction (clotting and mating) does not take place at once, but only after a period of time, which may be one to several days, during which the two clones live intermingled in the same culture.

Such a difference in readiness to react is often found between the original and the derived mating types resulting from self-differentiation of a clone. The first case observed was in the clone 2H34b of Variety I. This was almost certainly of the mating type B. From it, thirteen split pairs were obtained and from *a* and *b* of each, clones were derived (December 1-14, 1939). On December 10 tests were made for three of the split pairs (6 clones). By the second day of the test one member of each pair had reacted fully (with three of the tester types), while the other member had not. All those that had thus fully reacted were of the original mating type B. The other member (derived type D) of each pair did not fully react till several days later. Thus the original type conjugated more readily than the derived type.

Of the other ten pairs tests were made December 14. In six of them the original type B reacted first, while the derived type D did not react first in any case. That is, in nine of the thirteen split pairs the original type B reacted a day or more before the derived type D, while in four of them the two reacted on the same day.

Thus the animals which remain of the original type (B) are prepared to react at once. But the process by which the derived type (D) has been produced from the original type has in some way weakened the tendency to react; so that a period of a few days is required before the derived type has again attained its full reactivity.

This difference in the two types as to the strength of the tendency to react appears most decidedly when the tests are made early, within a few days (three or four) of the time that *a* and *b* were isolated.

Other instances of a difference in readiness to react between the two types resulting from self-differentiation are the following (in all cases in which a certain clone is stated to react earlier or more readily than its mate, this means that it reacted at least 24 hours earlier; often more than 24 hours earlier).

Clone 2H54b (Variety I). Twenty-two split pairs, yielding forty-four clones; in each case one member is type B (original), the other D (derived). The original type B reacted first in twelve cases; the derived type D did not react first in any case. The two reacted at the same time in ten of the 22 pairs.

Clone 2H51a, of Variety I. Self-differentiation produced the two types B (original) and C (derived). Of the 8 split pairs obtained January 5 to 11, type B (original) had by January 22 reacted in all cases (8), the type C (derived) in but three cases. A total of 40 split pairs were obtained from clone 2H51a. In 29 of these there was a difference of one to several days in the time of reaction of the two members. In every one of these 29 it was the clone of type B (original) that reacted first. In the remaining 11 pairs the two member types, B and C, reacted on the same day.

It will be recalled that in this case (Clone 2H51a) the original type B has longer and more slender individuals, and these multiply more rapidly than the shorter thicker individuals of the derived type C. The two types produced by self-differentiation thus differ in this case in four observable ways: in mating type, in form and dimensions, in rate of fission, and in strength of the tendency to conjugate.

Clone J17b1 (Variety I). Twenty-nine of the sixty split pairs were tested as to readiness to react. In 25 of the 29 the original type B reacted first: the two reacted at the same time in 3 cases, while D reacted first in one case.

Clone LP10 (Variety I). Of the six split pairs in every case the member that was of the original type D reacted several days before the one that was of the derived type C.

In Variety II, the original type (H) was observed to react more readily than the derived type (E) in the clone NH13. There were numerous other clones, of Varieties I and II, in which a difference in readiness to react could not be found.

To summarize, self-differentiation of a clone gives rise to individuals which may differ in four different ways: (1) in mating type; (2) in size and form; (3) in rate of multiplication; (4) in readiness to conjugate. The only one of these that is to be observed in all cases is the difference in mating type.

In Variety I, greater length and slenderness, a higher rate of fission, and a greater readiness to

conjugate belong to the original type; the derived type being shorter and thicker, slower in fission, and less ready to conjugate. In Variety II, so far as observed, the relations are the same, save that in some cases at least it is the derived type that has the larger individuals and divides more rapidly.

8. Relation of Self-Differentiation of Clones to Constitution of Wild Populations. Collections from a particular body of water often include just two mating types, such that when one of these two types undergoes self-differentiation, it produces the other. Examples of this are the following:

(1) On November 22, 1939, I received from Doctor T. M. Sonneborn a collection of *Paramecium bursaria* from a pond at Morgan, Monroe State Forest, Indiana. These were designated Mo. The animals belonged to Variety II; some were of type F, others of type M. Two clones of each of the two types were cultivated. All four underwent self-differentiation, the two F clones produced the additional type M, the two M clones produced the additional type F. Apparently, therefore, the entire population was of the constitution (FM), some being F(M), others M(F). Either could by self-differentiation produce the other.

(2) From a pool in the grounds of the Del Monte Hotel, Monterey, California, came a collection known as DM. It included only individuals of two of the types of Variety I, namely C and D; of 60 clones, 44 were C, 16 were D. One of the D clones (DM13) underwent self-differentiation; it produced the derived type C. It seems probable that the population was, therefore, of the constitution (DC), some being D(C), others C(D), either transformable into the other.

(3) From a gold-fish pool at Westwood Hills, Los Angeles, was obtained a population designated Br. The Br population included only the types B and C of Variety I. Of 30 clones, 17 were of type C, 13 of type B. One of the clones (Br48) that was of the B type underwent self-differentiation: it produced then the other type C. The constitution of the population was presumably (BC), some of the clones being B(C), others C(B).

(4) A collection obtained from a pool in the Botanical Garden of Johns Hopkins University consisted of clones of the two types E and F of Variety II. One of the clones (JH2) underwent self-differentiation, producing both E and F.

Later, the E type produced anew F, while the F type produced anew E, as before set forth.

It is however by no means always the case that a wild population consists of but two types, either transformable into the other. In the population *He*, of twelve clones, five were of type A, six of type D (and when D differentiated it produced A): but there was one clone of type B. The population *Lo*, from a pool at Baltimore, included representatives of all four mating types of Variety I. A population *St* from Staunton, Virginia, included representatives of four types of Variety II, types E, G, H and J. A population *Sw*, from a pool near Cockeysville, Maryland, included all the 8 mating types of Variety II.

EFFECTS OF SELF-FERTILIZATION AND OF INBREEDING

Clonal self-differentiation, its nature and what it reveals as to the constitution of the stock has up to this point been the center of interest. A similar examination is required for self-fertilization, particularly as to its effects on the clone or stock that undergoes it. Self-fertilization is a particular case of inbreeding; with it must be treated consequences of close inbreeding that are not precisely due to self-fertilization.

As before set forth, self-fertilization occurs but rarely in clone cultures. It is, therefore, impossible to procure from such cultures self-fertilized pairs in such numbers as are required for genetic study. This difficulty is met by the use of split pairs. If from a clone culture even a single split pair is obtained (in the way described on earlier pages), this will furnish at any time as many self-fertilized pairs as are desired. Two members of the split pair are cultivated separately, each yielding a clone. The two clones, like their parents, are of different mating types. When individuals of the two clones are mingled, they conjugate, thus providing unlimited numbers of the pairs that result from clonal self-fertilization.

Among other effects, clonal self-fertilization alters the mating types present in the clone. Inheritance of the mating type in self-fertilization and in inbreeding must therefore be first presented. In giving an account of this, only matters particularly germane to self-fertilization and inbreeding will be taken up, reserving the general phenomena of inheritance for a later paper.

INHERITANCE OF THE MATING TYPES IN SELF-FERTILIZATION AND INBREEDING

Self-fertilization has been observed, with its results so far as concerns the mating types produced, in clones of all the four mating types of Variety I. In some of the types the number of observations is few; in others it is adequate for determining the nature of the results.

Self-Fertilization in Mating Type D.

The consequences of self-fertilization have been most fully observed in clones of Type D. These are as follows:

(1) The H Stocks. The H stocks are a succession of clones and pairs all descended from the single individual *He6*, of mating type D. Their history illustrates particularly well the phenomena and results of clonal self-fertilization. The successive clones and pairs are the following.

H Pairs. As before set forth, on May 4, 1938, the clone *He6* of Variety I (derived from a single individual of April 21, 1938) underwent self-fertilization. It was of mating type D; by self-differentiation it had produced the additional type A. The individuals of the two types then conjugated (May 4), so that the two individuals of each pair are of mating types D and A respectively. Forty-eight pairs so formed were isolated May 4, and numbered H1 to H48 (two were later discarded, so that the final number was 46). The two members of the pairs separated during the night of May 5. The two ex-conjugants were then isolated, one being designated *a*, the other *b* (this on May 6). There was no fission till the night of May 7; all the ex-conjugants then divided. There was thus a period of seventy-two hours or more from the time the pairs were isolated until the first fission. This makes it certain that conjugation had been consummated in all the pairs, since individuals that have not conjugated divide every twenty-four hours, or oftener.

The two products of fission of the ex-conjugants *a* and *b* were isolated as *a1* and *a2*, *b1* and *b2*. Thus from each pair four clones were cultivated, each receiving a distinctive designation, as H1a1, H2b2, and the like. The total number of clones cultured from the final forty-six pairs was thus 184. These were cultivated under favorable conditions, each in a small vessel of lettuce infusion seeded with a single species of bacterium, as described in my earlier communication (1939). In this medium, individuals that

have not conjugated flourish and undergo fission at least once every twenty-four hours.

The majority of the ex-conjugant clones flourished, and multiplied at about the rate just mentioned. But as is usual after conjugation, a number of the ex-conjugant clones after a time ceased to multiply, became abnormal or weak, pale and thin, and finally died. It is notable that usually the four clones from any pair have the same fate; if any of them weaken and die, all four do so. The four clones of a single pair are of course cultivated independently; they are no more alike in their environment than are any four taken at random. The usual identical fate of the four appears clearly due to their common genetic constitution.

By May 25, three weeks from the time of conjugation, seventeen pairs (37 per cent of all) had thus died out completely, in all their four clones. There were thus left representatives of twenty-nine pairs. Six of these had lost one or more clones, two had lost one, three had lost two, one had lost three. In the rest the four clones all survived. Thus at this time there were left 105 clones, representing twenty-nine of the original forty-six pairs. Forty-three per cent of the clones had died out.

These 105 clones remained immature for long periods, varying from a little over a month to more than two years. In time all but three became mature (these three belonged to different pairs, and in each of these there were three other clones that reacted fully, so as to show the type to which the pair belonged). The clones were subjected to frequent tests with the four testers of Variety I, until the type to which each belonged had been determined. The results are as follows:

In every case all clones descended from any pair are of the same mating type. Of the four clones from any pair, two are descended from one parent, originally of type D, the other two from the other parent, originally of type A. Yet all four belong now to the same type. From Pair 1 the four clones are all of type A; from Pair 13 the four clones are all of type D; from Pair 46 the four are of type B.

The four clones from any pair are of course cultivated separately, and this separate cultivation continues for months, before the clones are mature. The four clones of any pair do not as a rule become mature at the same time. Yet with their separate cultivation for long periods and their separate testing at different times, it

finally turns out, when the results of all tests are finally tabulated, that the four clones of any pair belong to the same mating type, though those of different pairs may belong to different mating types. The common mating type of the four clones must therefore be the result of their common constitution immediately after conjugation. This common constitution might be due to chromosomal similarities brought about during conjugation. Or it could conceivably be due to certain environmental conditions operating during the time that the two members of the pair are united. In the latter case this environmental determination would have to be inherited in later fissions. In any case, it is clear that the exchange of pronuclei in conjugation has resulted in making the two ex-conjugants, that were of diverse mating types at the time of union, of the same mating type.

Of the twenty-nine pairs, fifteen gave descendants that were all of type A; thirteen gave descendants that were all of type D. Thus in twenty-eight of the twenty-nine pairs the descendants were of the same type as one of the two parents; approximately half like the A parent, half like the D parent.

But the remaining single pair gave descendants all of which were of type B. The two parents A and D give in this pair four clones that are of a different type from either.

The general result is then as follows: twenty-nine pairs, $D \times A$, yield after conjugation fifteen pairs that are A throughout, thirteen that are D, one that is B. Of the remaining type C of Variety I none were produced.

The appearance of the type B among the descendants (though in but one pair out of twenty-nine) is of interest. It will be recalled that the original clone from which all are derived by self-fertilization was of mating type D. It differentiated, producing the additional type A, so that the constitution of the original clone could be represented as $D(A)$. Now the two products of differentiation unite in conjugation. They produce in most cases again (as might be expected) the types A and D. But in one pair they produce the type B.

HH Pairs. Inbreeding was continued further by mating together one of the A clones and one of the D clones produced in the conjugation just described. This gave a second inbred generation of the H stock. The pairs so produced were designated HH. Four clones were cultivated from each pair, as in the first generation pairs.

The two parent clones A and D were mated September 1, 1938. From their union 57 HH pairs were obtained (September 2–September 4); the four clones from each of these were cultivated in the same way as the H pairs. In this second inbred generation mortality was much higher than in the first. By September 20, about two weeks after conjugation, 157 of the 228 clones were dead; that is, sixty-nine per cent had died. This mortality continued; by November 9, only 22 clones, representing 11 pairs, remained. When finally tested, half the clones were still immature. Eleven clones representing seven pairs were determined by tests. Five were of type A, two of type D. All the surviving clones thus in this case belong to one of the two parental types.

2H Pairs. Another second inbred generation was later obtained by mating on April 20, 1939, two more of the clones derived from the H pairs—one clone being as before of type D, the other of type A. Sixty pairs were isolated on April 24. Since it had by this time become clear that all the descendants of a single ex-conjugant are of the same mating type, only one clone was cultivated from each ex-conjugant, two (*a* and *b*) from each pair. There were thus one hundred twenty clones; these were called the 2H clones. Mortality was again high. By May 10 there remained but twenty-four clones, representing eighteen pairs. Of the sixty pairs, seventy per cent had died out completely. Of the one hundred twenty clones eighty per cent had died. Of the surviving eighteen pairs, ten were of mating type B, three of type A, two of type D; while in one pair one of the ex-conjugants gave clones of type B, the other of type A. Two of the pairs could not be determined with certainty because self-fertilization occurred in them before tests were completed.

Thus in this case, although the parents were again of types D and A, a large majority of the descendant clones were of type B. No clones of type C had as yet appeared among the descendants of the original self-fertilized D.

Self-Fertilization in Clones Descended from 2H.—The results of inbreeding were further studied through the occurrence of self-fertilization in five of the clones descended from the 2H pairs just summarized. These constituted a third generation of clone inbreeding. Each of the five was descended from a single ex-conjugant of 2H. From four of these five clones pairs and split pairs were obtained. These four were designated respectively 2H34*b*, 2H51*a*, 2H54*b*

and 2H58*a*. Some account has been given of these in the section on self-differentiation. They are likewise instructive for the study of inheritance of mating type.

The clones 2H34*b* and 2H54*b* differentiated before self-fertilization into the two types B and D, while 2H58*a* differentiated into B and A. The three types A, B and D have before appeared in the H stocks. But the clone 2H51*a* produced through self-differentiation the mating types B and C. This is the first appearance of the mating type C among the descendants of clone He6, of type D. By its appearance it is demonstrated that the single type D by self-differentiation, self-fertilization, and inbreeding among its descendants, is capable of producing all the four mating types A, B, C, D, of the variety to which it belongs.

As will be set forth further in the next section, very few pairs or clones survived (to become mature), in the pairs resulting from this third step in inbreeding. Out of a very large number of conjugant pairs, a total of but twenty-six clones survived to be tested. Of these sixteen were mature: all were either type B or type D. These add nothing significant to the knowledge of the genetics of the H stocks.

To summarize, the stock H began as a single individual of the mating type D, the entire stock descended exclusively from this individual, with no accessions from outside it. This individual produced by vegetative reproduction a clone which differentiated into the two mating types A and D. These conjugated, and among their descendants were clones of all the four mating types A, B, C and D. The single type D has the potentiality of producing all four mating types.

Other consequences of inbreeding that are illustrated by the history of the stock "H" are set forth in a later section.

The DM Stock. Sixty clones were obtained from sixty individuals collected December 24, 1939. These were designated DM. In one of these clones, DM13, of the mating type D, self-differentiation occurred into the two mating types D and C. A single split pair consisting of these two types was obtained January 31, 1940; the two types were isolated as two clones. On March 23, 1940, these two were mated; from them one hundred and two pairs were obtained. As usual many of these died or remained immature for many months. Up to the present time, (April 17, 1941) the mating type of thirty-one

of these pairs has been determined; fifteen were of type D, thirteen of type C, two of type B, one of type A.

Thus the single individual DM13 of type D gave origin by self-fertilization to clones of all the four different types of the variety to which it belongs (Variety I).

Self-Fertilization in Mating Type A.

Clone 881a. This was derived from a cross of the two cones *l* and *m* of the mating types A and C respectively. It was itself of the mating type A. On October 19, 1937, it underwent self-fertilization. Of five pairs which it produced, three were of type A, one of type B, one of type D. Thus from a clone of type A, three of the four types of Variety I were produced.

Self-Fertilization in Mating Type B.

As shown in Table 1, different clones of the mating type B may yield at self-differentiation as the derived type either A or C or D, so that from type B all the four types are derived. But from any single clone of type B, the production of only one additional type has thus far been observed. A typical case is the following:

Clone Br48. This clone was originally of type B. It underwent self-differentiation into the types B and C. These two conjugated. Twenty-three pairs produced descendants that were tested. Of these, nine were of type B, fourteen of type C. Thus all descendants were of one of the two parental types.

Self-Fertilization in Mating Type C.

Clone *m* of mating type C. Five pairs were produced by self-fertilization in this clone. Two pairs yielded descendants of type C, while three gave descendants of type B.

Clone Wat1. This was a clone originally of mating type C, derived from a single individual of July 12, 1939. It underwent self-differentiation and self-fertilization, producing among its descendants clones of the three types A, B and C (see the fuller account in a later section).

From the above it is obvious that fully adequate observations exist only for clones of type D. But certain positive facts emerge from the observations in all four types. These are the following:

A clone of type D may yield by self-fertilization descendants of all the four types A, B, C and D.

A clone of type A may yield by self-fertilization descendants of the three types A, B and D.

Of type B, a single clone is thus far known to produce only clones of types B and C. But different clones of type B have produced in different cases A, B, C and D.

Clones of type C may produce by self-fertilization clones of the three types A, B and C.

It is possible that more extended observations will show that clones of types A, B and C may each produce all the four types that occur in the variety.

STERILITY IN LATER INBRED GENERATIONS

As earlier mentioned, a considerable number of pairs from self-fertilized clones die after conjugation without producing descendants. In the H stocks, after the first self-fertilization thirty-seven per cent of the pairs died without producing descendants. When clones resulting from this self-fertilization were mated together (in the pairs HH and 2H), 70 per cent failed to produce descendants.

Of the clones that did survive after this second inbreeding, four underwent self-fertilization, thus constituting a third successive close inbreeding in the stock derived from the single individual He6. The pairs from these self-fertilizations were still less fertile than earlier. Their history is as follows:

The clone 2H34b underwent self-fertilization during the first twelve days of December, 1939. From it were obtained at that time fifty pairs, of the types B \times D. All died within four days.

During the same period the clone 2H54b underwent self-fertilization, yielding pairs B \times D. Of these pairs forty-five were obtained, the two-exconjugants of each pair being cultivated separately. All the ninety clones from the exconjugants died within a few days, except two, belonging to different pairs. The survivors were clone 30 of type D, and clone 32b of type A.

January 6 to 26 the clone 2H51a underwent self-fertilization, yielding pairs B \times C. Of these pairs, one hundred and thirty-five were isolated and cultivated in the usual way. All except two died within a few days, in most cases without dividing. The two that survived were of type B.

In the cases just described, the method of cultivation was that which was most successful in other cases, and many other clones, not derived by inbreeding, were flourishing in the same culture medium at the time these died.

This very high mortality, or lack of fertility, after three inbreedings appeared of interest, so

TABLE 3

Results of self-fertilization and inbreeding. Pairs from self-fertilized clones descended from the inbred pairs 2H. Third inbreeding in the stock.

Self-Fertilized Clone	Date of Self-Fertilization	Number of Pairs	Mating Types of the Pairs	Result
2H54b	Dec. 1-13, '39	45	B × D	All died but 2
2H34b	Dec. 2-12, '39	50	B × D	All died
2H51a	Jan. 6-26, '40	135	B × C	All died but 2
2H58a	Jan. 27, '40	48	B × A	All died
2H51a	Jan. 27, '40	48	B × C	All died
2H34b	Jan. 27, '40	24	B × D	All died
2H54b	Jan. 27, '40	24	B × D	All died
2H51a	Jan. 24-Feb. 8, '40	60	B × C	All died
2H54b	Feb. 9, '40	48	B × D	18 clones survived (13 pairs)

Total number of pairs 482, of which 17 survived (3.5 per cent).

that additional self-fertilizations were made, using the same methods of cultivation. The results of these are summarized in Table 3. In this table are included for completeness the three cases just described.

Only one of the self-fertilized clones, namely clone 2H54b, yielded pairs that survived in any appreciable number. From this clone a total of one hundred and seventeen pairs were obtained. There survived representatives of fifteen of these, so that one hundred and two of the one hundred and seventeen pairs died without coming to maturity; a mortality of 87 per cent. Also, in clone 2H51a there survived representatives of two pairs out of two hundred forty-three included in Table 3. In the other self-fertilized clones the mortality was one hundred per cent.

It seemed desirable to determine so far as possible whether the death of the ex-conjugants was the consequence of anything in the nutritive conditions. The organisms were living in the lettuce culture medium to which bacteria of a single species had been added, as described in my former paper (1939). It had been found that the addition of an algal culture, as described in the paper just mentioned, is unnecessary. The organisms flourish equally well without the algae.

It was noticed however that organisms living among filamentous algae in ponds are somewhat larger, deeper in color, and seemingly more robust than those in the lettuce medium. If filamentous algae such as *Spirogyra* were added to the lettuce medium, it was found that in the course of a week or two the animals take on the deeper color, slightly larger size, and generally more robust appearance seen in the animals collected from ponds.

Will the inbred animals flourish better after

conjugation if cultivated before and after with the filamentous algae? This seemed a possibility, so that cultures of the inbred stocks were prepared in which this condition was fulfilled. The inbred clones were first cultivated for some weeks in lettuce infusion to which had been added filaments of *Spirogyra* or of some other filamentous algae. The animals took on the expected deeper color, larger size, and more robust appearance. They were then mated as before. Part of the matings were of the two members of split pairs from the same clone; these were therefore pairs from self-fertilization of the 2H clones, descended by inbreeding from the clone He6. A number of matings were made also between the different inbred stocks derived from the 2H pairs. After conjugation the ex-conjugants were further cultivated in lettuce infusion containing filamentous algae. The chief data for these matings are given in Table 4.

Table 4 shows that culture in a medium containing filamentous algae, although it makes the individuals more robust and deeper in color, does not increase the rate of survival after conjugation in the clones that have been deeply inbred. The use of *Spirogyra* or other filamentous algae in the culture medium was therefore discontinued.

Further experiments were made to test the results of crossing the inbred clones. Crosses were made of the inbred clones with each other, and of the inbred clones of the H stocks with the unrelated stock Br48. The H stocks came from Maryland, while the Br48 stock was collected in California. The further experiments involving comparisons between the results of self-fertilization or clone inbreeding, and outbreeding, are set forth in the following paragraphs.

Clone 2H58a. In Tables 3 and 4 it is shown

TABLE 4

Results of self-fertilization and inbreeding in pairs derived from self-fertilized clones of the 2H stock, when cultivated in a nutrient medium containing filamentous algae. Animals robust and deeply colored.

Mating	Date of Mating	Number of Pairs	Mating Types of the Pairs	Result
2H58a self-fertilized	Feb. 2, '40	38	B × A	All died
2H58a self-fertilized	March 11-18, '40	62	B × A	All died
2H54b self-fertilized	March 17, '40	48	B × D	All died but 1
2H58a × 2H51a	March 16-23, '40	51	A × C	All died
2H54b × 2H51a	March 12, '40	24	B × C	All died
H38b2 × 2H51a	March 16, '40	3	C × D	One survived

that self-fertilization in the previously twice inbred clone 2H58a results in the death of all the pairs produced. This clone was crossed with the related 2H clone 2H51a (Table 4), and again the mortality was one hundred per cent.

The clone 2H58a was now outcrossed twice to clones of the unrelated stock Br48. In both crosses 2H58a is of the mating type A. In the first outcross the stock Br48 was present as the mating type C, in the second as the mating type B. The results for all the matings of clone 2H58a are as follows:

Thus in the clone 2H54b, outcrossing with the Br48 stock greatly increased the percentage of pairs that survived.

On their face the experiments just described appear to show clearly that close inbreeding greatly decreases the fertility in *Paramecium bursaria*. After the first self-fertilization the fertility of the stocks was in some cases relatively little impaired. In the H pairs after one self-fertilization the mortality among the pairs was thirty-seven per cent; in the DM stocks, 37.5 and 8.6 per cent respectively; in the stock of

Mating	Date of Mating	Number of Pairs	Mating Types of the Pairs	Result	Percentage that Survived
2H58a self-fertilized	Feb. 2, '40	38	B × A	All died	0
2H58a self-fertilized	Mar. 11-18, '40	62	B × A	All died	0
2H58a × 2H51a	Mar. 16-22, '40	51	A × C	All died	0
2H58a × Br48	April 10, '40	191	A × B	70 survived	36.6
2H58a × Br48	April 10, '40	71	A × C	69 survived	97.2

As this tabulation shows, outcrossing of the clone 2H58a to the clone Br48 raised the percentage of survival from 0 to 36.6 in one case and to 97.2 in the other.

Similar comparisons of inbred and outbred pairs were made for the clone 2H54b. In this clone mortality after self-fertilization was not in every case complete, though it was very high. The effects of outbreeding with clones of Br48 are shown in comparison with the effects of self-fertilization in the following:

J17b1, however, it was 87.5 per cent. After a second inbreeding the mortality was higher; about 70 per cent for the pairs HH and 2H. After a third inbreeding the mortality in the pairs rose in most cases to 100 per cent. Outcrossing greatly decreased the mortality.

Yet the exact interpretation to be given to these facts is less certain than first appears. At the later inbreedings the stocks differ from the earlier ones in other ways besides the fact that they have been repeatedly inbred. They are

Mating	Date of Mating	Number of Pairs	Mating Types of the Pairs	Result	Percentage that Survived
2H54b self-fertilized	Dec. 13, '39	45	B × D	All died but 2	4.3
2H54b self-fertilized	Jan. 27, '40	24	B × D	All died	0
2H54b self-fertilized	Feb. 9, '40	48	B × D	All died but 13	27.1
2H54b × Br48	Apr. 10, '40	72	B × C	36 survived	50.0
2H54b × Br48	Apr. 10, '40	72	D × C	64 survived	88.8
2H54b × Br48	Apr. 12, '40	108	D × B	85 survived	78.7

older in elapsed time; and they have been longer under cultivation in the laboratory. To both of these conditions importance has been attributed by certain authors for reducing the vigor and vitality of the stock. There are indications that one or both of them may play a role in the results. An extended study has been made of mortality after conjugation. It will therefore be best to reserve this matter for treatment in a paper to be devoted to clonal youth and maturity, age and death.

EFFECT OF CLONAL SELF-DIFFERENTIATION AND SELF-FERTILIZATION ON THE STOCK

After self-differentiation and self-fertilization have occurred in a clone, the clone is evidently no longer "pure"; that is, its members no longer all have the same genetic constitution. By self-differentiation part of the clone has transformed into a different mating type, and there are other changes.

Yet we have in the laboratory many cultures of clones that have been cultivated here for one to four years, and have presumably undergone self-differentiation one or more times (some are known to have done so), yet they still react as the same mating type as at the beginning. Clone *l* has been in the laboratory for four years. It originally reacted as mating type A. It is known to have undergone self-differentiation, since pairs were observed in it February 4, 1938. It still reacts as type A. Clone *m*, originally of mating type C, has likewise been in the laboratory four years, and is known to have undergone self-differentiation, since pairs were obtained from it July 14, 1937 and January 15, 1938. Yet it still reacts as type C. Similar relations exist in the clone *1b*, produced from an ex-conjugant of June 18, 1937; it was of type D and still remains so (April, 1941). Many other clones could be cited in which the facts are parallel to those just mentioned. In spite of the occurrence of self-differentiation, the clones remain of the same mating type as at first.

On the other hand there are also in the laboratory clones which have long been under cultivation and which no longer react as they formerly did. Some cease to react at all (for a time, at least). Others when tested react as a different mating type from that which they at first evidenced. Examples will be given later.

To understand how these and other results are produced, keep in mind a clone culture in a small vessel, such as is used in the laboratory. It con-

tains thousands of individuals that are all of the same mating type, and of similar morphological and physiological properties. They are of similar size and form, multiply at about the same rate, and show mating reactions with about the same readiness. Self-fertilization occurs in this culture. What changes does it induce?

The essential nature of the changes produced has been dealt with separately on earlier pages. Here it is their effect on the culture that is presented.

The occurrence in the clone of self-differentiation brings about of course the appearance in the culture of a number of individuals of a different mating type. The clone is no longer uniform with respect to mating type. In many cases, too, as before shown, the individuals of the new mating type differ morphologically and physiologically from those of the original mating type. The clone, originally uniform in its genetic constitution, is no longer so. This period, in which the clone culture contains two mating types, lasts but a short time. If at this time single individuals are taken from the culture and tested, some will be found to be of one type, some of the other. Thus, the clone NH13 was originally of the mating type H. A few pairs were observed in it July 6, 1940. On that date ten single individuals were taken from it and cultivated till they produced clones; these were then tested. Four were of the original type H, while six were of the newly produced type E. It is at this stage of course that "split pairs" may be obtained from the culture. If at this time the clone is tested as a single population, it will be found to react with all of the types of the variety. One of the two mating types present reacts with all but one of the testers: the other likewise with all but one, including the tester type with which the first does not react. Such reaction with the testers of all the types occurs very rarely, but if a clone is tested immediately after self-differentiation, it will be observed.

Next occurs self-fertilization; the individuals of the two mating types unite in pairs. After about forty-eight hours they separate. The ex-conjugants reproduce by fission, but their descendants are now immature, so that they do not take part in the mating reaction. If, as is commonly the case, relatively few pairs have been formed, this lack of reaction in their descendants will have no noticeable effect on the reactions of the culture. When tested it will continue to react as before, to three of the testers,

not to the fourth. It consists mainly of individuals of unchanged mating type, though its reactions are a little diluted, as it were, by the presence of a number of individuals that are immature and do not react. This is part of the secret of the retention by a clone culture of its original mating type reaction, even after self-differentiation and self-fertilization have occurred. Other relations play a role in this result; they are to be mentioned.

If self-differentiation has occurred very generally throughout the culture, so that two types are present in about equal numbers, then after the conjugants have separated, practically all the individuals will be immature, so that the culture will not show any mating reaction when tested. This situation arises but rarely, but it has been observed in a number of cases. Thus, during the period January 24 to 28, 1941, tests were made of 217 clone cultures of Variety II, which had been in the laboratory for periods of from several months to four years. All had formerly reacted actively and the mating type of each was known. Of the 217, ten now did not react at all. Their individuals were immature as a result of self-fertilization in the clone.

The condition of immaturity lasts for a long time—months or years; during this long period the descendants of the self-fertilized pairs do not react. In time, however, they begin to reach maturity. They now begin to take part again in the mating reaction. As shown above, different pairs give rise to descendants that are of different mating types. Two or three or even all four of the mating types may now be present in the culture that was originally made up of a single clone of a single mating type. The individuals of different mating type unite in pairs. Again we have the appearance of pairs in the single clone culture, but now the pairs are not all of the same combination of mating types, as they were at the time of the first self-fertilization in the clone. Some pairs may be of types A + B, others of A + C, A + D, B + C, B + D, or C + D. If split pairs are obtained at this stage, they are no longer of two types only; they may (in Variety I) be of any of the combinations just mentioned. The originally single clone has now taken on the constitution of a wild population.

This situation is very rarely encountered, and of course only in old clones that have been a long time in mass culture in the laboratory. I have observed it but twice. One case was in the stock Gr13 of Variety II. This was originally a clone

of mating type K, derived from a single individual of February 25, 1938. Pairs were observed in the mass culture November 12, 1940, after it had been cultivated in the laboratory for two years and eight months. From it were obtained thirty split pairs. Of these twenty-nine were of K and M, while one was of M and G.

The second case was analyzed experimentally. It occurred in the stock Wat1, of Variety I. This was originally a clone of mating type C derived from a single individual collected July 12, 1939. In the mass cultures of this clone pairs were observed from December 9, 1940 to February 2, 1941: thus after eighteen months of cultivation. From these cultures 38 split pairs were obtained. Of these, 14 were a combination of A and C, 15 were A and B, and 9 were B and C. At this time therefore the cultures contained three of the four mating types of the variety; namely types A, B and C. These three combined in pairs in the three possible ways AB, AC, BC.

This case was analyzed by obtaining from the cultures new clones beginning with single individuals and keeping these clones under observation until the first self-differentiation and self-fertilization occurred. Two new clones were obtained, from the individuals S6b of December 19, 1940 and S13a of January 3, 1941. Each underwent self-differentiation less than a month from the time the clone was started, and now, as was to be expected, each produced pairs of but a single combination of mating types. The clone S6b was originally of the mating type B. The split pairs from it, nine in number, were all of the combination B and C. Of the clone S13a the original mating type had not been determined when self-differentiation occurred. The split pairs from it, twelve in number, were all of the combination A and B. Thus clones derived from a single individual by primary self-differentiation produce pairs that are all of the same combination of types, as in all cases listed in Tables 1 and 2.

When a stock contains individuals of a number of different types, as in the case of the stock Wat1, described above, the different types tend to unite in conjugation, their descendants being immature. All become thus immature, so that they no longer react, except in the case of the mating type that was in the majority. Not all of its members can find mates, so that there remain a number that have not been reduced by conjugation to sexual inactivity. These are the only individuals of the culture that react, and since they all belong to the same mating type,

the reaction of the culture as a whole when tested is that of their mating type.

But the results of self-fertilization in a clone are greatly modified by the fact, demonstrated on previous pages, that after self-fertilization a large proportion of the ex-conjugant clones die—either before or after division of the original ex-conjugant. The few that survive multiply and replace the clones that die. When these become mature the culture will upon test be found to be of the mating type that is characteristic of the clone or clones that have survived. Since the largest proportion of the new clones produced at conjugation belong to the same mating type as one or the other of the two parental types, the survivors will usually be of one of the parental mating types. There may survive but a single clone of one of the parental types, or more rarely, a single clone of one of the other types. In the latter case the clone culture in its later history reacts upon test as a different mating type from its type in its earlier history. A few examples of such results have been observed. Thus, between January 17 and 22, 1941, there were tested 128 clones of Variety I, which had been cultured in the laboratory for many months, in numbers of the cases for years. The original mating type was known for all these cultures. In this testing of January 17–22, 1941, 123 of the 128 cultures reacted as they had at first, while in five cases the reaction was changed. Two clones that had at first reacted as type A now reacted as type C. Also, three clones that at first reacted as type D now reacted as type C. The change of reaction was doubtless brought about in one of the ways above described.

In concluding this section, the changes of reaction in both varieties at the testing of January 17 to 22, 1941, may be summarized. A total of 345 clones that had been cultivated separately for many months were tested; 128 were of Variety I, 217 of Variety II. All had earlier reacted sexually in a definite way, and the original mating type of each was known. At this later testing, eleven of the cultures did not react sexually; 10 of these belonged to Variety II, 1 to Variety I. Ten of the 345 cultures had changed in reaction type. Five of these belonged to Variety I, five to Variety II. Of Variety I, two clones had changed from A to C, three from D to C. Of Variety II, five had changed from type K to type G. In this latter case the five clones had originally come from one,

of type K, so that possibly the five should be considered but one case of a change of type.

Discussion of the more general problems raised by the phenomena described in the present paper is reserved until other pertinent matters have been presented in later papers.

SUMMARY

1. As a rule all members of a single clone belong to the same mating type, since the type is inherited without change in ordinary reproduction by fission. Hence usually members of the same clone do not conjugate together.

2. But on rare occasions conjugation is found to occur among members of the same clone ("self-fertilization" of the clone).

3. Self-fertilization occurs within clones of *Paramecium bursaria* only at long and seemingly irregular intervals. In this it is like endomixis, so that it appears probable that the two are connected. Observation indicates that on the average clonal self-fertilization occurs once in about two thousand culture-days.

4. The number of pairs to be observed in a clone culture undergoing self-fertilization varies in different cases from one or two to a number that includes most of the population.

5. The individuals of a clone that unite in conjugation are found by testing members of "split pairs" to be of different mating types. One is of the original type, the other of a different type.

6. Thus before clonal self-fertilization occurs part of the individuals of the clone transform into a different mating type ("self-differentiation" of the clone). Clonal self-differentiation results in a pair of types, one original, the other derived.

7. Self-differentiation of any clone yields in all the pairs the same two mating types.

8. Self-differentiation of different clones of a particular mating type yield in different cases different pairs of types.

9. The combination of two mating types produced by self-differentiation of any clone is characteristic for that clone.

10. Thus any clone is so constituted that it yields at self-differentiation a particular combination of two types. Its constitution is therefore in some sense double; one clone is D(A), another D(B), another D(C) and so on.

11. In Variety I, which has four mating types, A, B, C and D, clones of each of the six possible

combinations have been observed, AB, AC, AD, BC, BD and CD.

12. The two mating types produced by self-differentiation of a single clone may each by renewed self-differentiation produce again the same two mating types. Thus each is still double in genetic constitution.

13. The two clones resulting from self-differentiation of a single clone may differ in a number of ways. (1) They always differ in mating type. (2) They often differ in size and form; (3) often in rate of fission; (4) often in readiness to conjugate. In Variety I the individuals of the clone that is of the derived type are commonly shorter and thicker, divide less rapidly, and are less ready to conjugate.

14. Populations collected from a given locality frequently (not always) consist of just two types, either of which may by self-differentiation produce the other.

15. By conjugation of the two types produced by clonal self-differentiation, additional mating types may be produced. In Variety I a single clone of type D may thus produce all the four types (A, B, C, D) of the variety. Clones originally of types A, B, or C have been observed to produce by self-differentiation and self-fertilization three of the four types that occur in the variety.

16. A considerable proportion of the pairs produced at self-fertilization are usually sterile; they die without producing descendant clones.

17. After two or three successive self-fertilizations in the same stock, usually all or nearly all the pairs are sterile.

18. A clone culture originally reacts sexually as a single mating type; that is, it reacts sexually with all but one of the mating types of the variety to which it belongs. After self-differentiation and self-fertilization have occurred in the clone, the sexual reaction of the culture may or may not be changed. The following situations occur:

(a) After self-differentiation, but before self-fertilization, the culture contains two mating types instead of one. It therefore reacts sexually with all the mating types of the variety.

(b) After self-fertilization is completed, part or all of the clone is for a long period immature,

so that it does not react sexually. If but a part of the clone is immature, the reaction of the culture as a whole is the same as at first, though fewer individuals react.

(c) When, following self-fertilization, the ex-conjugant clones have become mature, the culture may contain several mating types. In time, these conjugate together and their progeny become immature, except for the "left-over" individuals of the most abundant mating type. The reaction of the culture as a whole is then that of this left-over type. This may be the same as the original type, or may be a different type.

(d) In most cases, the clone cultures as a whole retain their sexual reaction as of the original mating type, for very long periods. In the course of months or years a small proportion of the clones change their reaction type, in the way set forth.

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THE "MULE" PHEASANT¹

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ABSTRACT

One Ring-neck "Mule" pheasant in the breeding season exemplified the earliest, another the most advanced stage of change from female to male sexuality and plumage. Both, like hen-pheasants generally, had bilaterally well-developed vasa deferentia and epididymides. One had many seminiferous tubules in both right and left "ovaries", not open to the epididymides, varying from infantile or quiescent tubules to those undergoing spermatogenesis to spermatids only, and probably recovering from degeneration due to back pressure. It had two oviducts (the right smaller) in conditions indicating male without female sex-hormone activation, like that in ovariectomized fowl or in castrate Night Herons injected with testosterone propionate. The other had but one "ovary" with many cyst-like cavities suggesting that oögonia and small follicles had undergone lipoidal degeneration and been leached out by reagents, and a few testicular tubules apparently too infantile to respond to gonadotropic hormones as the other's had done. Its single (left) oviduct, merely a groove anteriorly and infantile posteriorly, showed no signs of hormone activation. These "mules" appear to exemplify in pheasants phases of female intersexuality (Goldschmidt) from crossing species stronger or weaker in sex-differentiating factors in which female-differentiating factors fail in embryonic, juvenile, or early adult life, with early or later development of male plumage, head-furnishings, and spurs, and various states of gonads and secondary sexual apparatus. The unstable equilibrium may be due to wideness of cross as in gonadless and intersexual hybrid Doves. In one, somatic non-disjunction may condition dorsal and ventral distribution of female and male feathers. The intersexual gonads and oviducts are responsive to seasonal cyclic gonadotropic stimulation and become active in the breeding season when not too infantile.

INTRODUCTION

BISSONNETTE (1940) described the plumage features and reproductive organs of a "mule" pheasant, properly preserved for histological study, in January, and the sex-glands of another found dead in October. These were compared with homologous parts from a normal hen-pheasant preserved at the same time as the January "mule".

Macroscopically the sex-glands of both "mules" were ovaries in autumn and winter condition of regression. Histologically neither exhibited any

eggs or ovarian follicles. In both, one or more regions might be interpreted as regressed follicles, as recovery sites or scars from cyst-like foci of infection, or from degenerated seminiferous tubules. They were pigmented like normal ovaries but more heavily.

The properly fixed January gonad exhibited coiled seminiferous tubules in various regions containing what appear to be spermatogonia and Sertoli cells arranged about the periphery of the tubules like those of male pheasants in January. The October gonad was so poorly preserved that fine histological structure could not be distinguished. In both birds, the paucity of proper ovarian tissues accounts for the "male" feathers of the mixed plumage; and the testicular tissue in one of them for the maleness of head furnishings and the slight enlargement of spur rudiments.

It was not known whether these birds had shown the mixture of male and female feathers and secondary sex-characters from hatching or had acquired the "male" characteristics after exhibiting completely "female" characters and behavior. So the question was left open as to whether they were intersexes or sex-inverts.

The question was raised as to whether these testicular tubules, in a gland otherwise ovary-like in structure, could respond to environmental conditions in the breeding season, undergo spermatogenic activity, and activate the oviduct and the vasa deferentia (two of which are present in the normal hen-pheasant, as well as in the "mules") and cause the assumption of the breeding phase of head furnishings characteristic of the cock. The search for other "mules" was continued in the hope that they might aid in settling these problems.

Continued interest in this anomaly by A. G. Csech, of the Game Warden Service of the State Department of Fisheries and Game, and of pheasant breeders, brought us two new specimens in good living condition, except as stated. One was more male-like in plumage and spurs than the earlier ones and was said to be mixed in feathering from the start. The other, less male-

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like, was undergoing change from almost completely female feathering toward that of the male. They are reported here because their histories are better known and dissimilar, and they consequently throw more light on the problems mentioned above.

MATERIAL AND METHOD

One of these "mule" pheasants (no. 3 in our series) was given us by Fred. Roach, pheasant breeder, of Simsbury, Connecticut, on April 19, and sacrificed for study on April 23. It was the most male-like of those so far seen; was in full feather and almost complete breeding plumage (Figs. 1, 2, 3, 4, 5).

The other, no. 4, was the least male-like "mule" we have seen; but definitely a "mule" when secured from the Bushy Hill Game Farm, Simsbury, Connecticut, on May 20. It had been kept in a pen of chicken wire and its frequent attempts to fly through the wire, when frightened, had worn off the feathers, skin, and flesh from the top of its head, leaving the skull bare and dry over an area of about three-quarters of a square inch (Figs. 7, 8). In spite of frequent tearing open of the wound, the bird lived in this condition for more than six weeks, until killed for study on June 11.

The complete urogenital systems, keeping both sides together, and the thyroids were removed from each "mule" immediately after skinning and fixed in Bouin's fluid. Kidneys, adrenals, ovaries, oviducts, epididymides and vasa deferentia to the cloaca were included. The whole system of no. 3 was photographed after washing out the fixative (Fig. 9), divided sagittally and across the middle, and each side sectioned serially transversely at 10 microns. The two sides of no. 4 were folded so that they faced each other and sectioned transversely in one series. Photomicrographs at suitable magnifications of representative sections from each bird were made after iron-hematoxylin and faint eosin staining.

OBSERVATIONS

"MULE" No. 3

External Characters

No. 3 was hatched in spring, 1939, a cross of Mongolian with Ring-neck or Black-neck; Mongolian characters, such as light iris, predominated. It had a crossed bill, was wild and fairly pugnacious. The feathers on crown, nape, back

of neck, shoulders, back, dorsum of tail and both wings were predominantly of female type. Consequently it lacked the two small tufts of feathers or "ears", erectile in the breeding male (Figs. 1, 2, 5). The rest of the body and the under parts of the tail were mixed male and female or predominantly male (Figs. 3, 4). The legs were small, like those of females, but the spurs were more highly developed than in the other "mules" or in normal females (Fig. 6). In size it was intermediate and nearer the male. Its behavior toward females was not noted. It was said to have given the male mating call.

Sex-organs

Its gonads bore no resemblance, in gross, to testes. On the left side was an ovary-like body with nodules, like small ovarian follicles in appearance, but fewer in number and not graded in size like those of a normal ovary. Another, similar, but smaller, narrower body on the right was nearer the mid-line. The left oviduct began as an infundibulum posterior to the "ovary" and lateral to the kidney, and extended to the cloaca with a marked fluid-filled swelling at the posterior ends of the kidneys (Fig. 9). A similar, but smaller, shorter, right oviduct exhibited a smaller fluid-filled enlargement. Both infundibula were delicate and difficult to discern in gross, but plain in sections.

Sections show that both right and left gonadal rudiments have developed and have been activated. They lack ova and follicles. Each consists of a stroma, pigmented like a normal ovary, in which coil several seminiferous tubules actively undergoing spermatogenesis with all stages up to and including spermatids, but not spermatozoa. Mitotic figures are numerous (Figs. 10-13a). In the left "ovary" is a cyst-like reticulum of cells with long processes and large vacuoles from which lipoidal substances have probably been dissolved out by technical reagents (Figs. 14, 15, 16). It contains no recognizable germ-cells. In some respects, it resembles degenerated mammalian corpora lutea, with degranulated cells and lipoidal products dissolved by reagents. But it seems more probable that it is a blind degenerate seminiferous tubule. It is the only structure in either ovary that would admit of interpretation as derived from a follicle or as representing remains of female germ-cells.

The testicular tubules of both gonads end blindly without connection to the epididymal

tubules and vasa deferentia. Some have lumina, some have not. They vary in condition from winter resting or infantile ones like those of the winter "mule" (Bissonnette, 1940) to those with almost breeding activity. Nests of germ-cells forming sex-cords rather than tubules are present and the germ-cells in them undergo spermatogenesis while in such positions (Figs. 12-13a).

Small lymphocytes have invaded some regions of both gonads and the left epididymis and vas deferens (Figs. 10, 11, 11a). The invasion is so great in some places that the tissues seem to be lymphatic in nature and in the process of developing into lymph nodes. All stages from small to large lymphocytes, and mitotic figures of dividing large lymphocytes are found in various places. In some, small lymphocytes invade the epithelial walls of the epididymal tubules and appear in the lumen. It is suggested that in some places they have cleared up or were clearing up degenerate tubules.² None of these regions occur in the right epididymis or vas deferens. Along the left they appear near the kidney, but not along the oviduct, in the mesentery of which the vas courses after leaving the wall of the ureter posterior to the kidney.

The left oviduct begins anteriorly as an open ostium just behind the "ovary" and extends to the cloaca. The endometrium of its distended region is not thickened nor activated as it would be by action of female sex-hormone. The right oviduct begins blindly somewhat posterior to the left. Although smaller it, also, is dilated with fluid and its wall resembles that of the left. The right vas deferens bears the same relation to the right oviduct as the left one does to the left oviduct.

Conditions of both oviducts (Figs. 9, 17) resemble those induced by testosterone propionate in castrate Black-crowned Night Herons and not those induced by estrogens (Noble and Wurm, 1940). It is worthy of note that Domm (1932) found distended oviducts in ovariectomized fowl and occasionally in those otherwise normal. This suggests that the small amount of gonadal material was secreting enough male hormone to cause the typical enlargement and distention of the two oviducts, while female hormone was scanty or wanting.

² We are indebted to Professor James E. Kindred for interpreting these lymphatic or lymphocyte-invaded regions and pointing out significant conditions there.

"MULE" No. 4

External Characters

No. 4 was much less cock-like than no. 3. It possessed the red region around the eye and the dark greenish black upper neck feathers. A small white neck ring incomplete dorsally and ventrally signified maleness. Because the top of its head was denuded to the bone, it was not possible to know what its condition otherwise would be. Male feathers and some intermediates were scattered among the predominantly female feathers on the rest of the body (Figs. 7, 8). A careful study of the plumage is deferred to a later time.

The bird was small, even for a female, and its spurs little, if any, larger than those of normal hens (Fig. 6). It was certainly undergoing change from female to male plumage and secondary sexual characters. Its behavior toward hens was not noted except that it dominated those kept with it since it began to assume other male characteristics. This is in accord with raised dominance in the peck-order of fowl injected with male sex-hormone (Allee, Colias and Lutherman, 1939) and with common observations on crowing hens in the barnyard, which are subservient to cocks, dominant to hens.

Sex-organs

No right gonad nor oviduct was found, nor any trace or rudiment from which either could develop. Remnants of the mesonephros formed well-defined but infantile epididymides on both sides with vasa deferentia leading to the cloaca (Figs. 18-23). These were much coiled anteriorly as far back as the posterior ends of the kidneys; closely related to the adrenals anteriorly and to the ureters posteriorly (Figs. 34-41). In some places are lumina containing colloid (Figs. 19-23), in others no colloid, and no lumina in others. They seem to be about equally developed on the two sides. Their linings failed of complete differentiation, and they end near the gonad (Figs. 18, 20). Among typical epididymal tubules are found some resembling testicular tubules (Figs. 20, 23).

Near the left adrenal and the ganglia in front of it was an infantile left ovary, with shallow cortex and flattened medulla, typical, except for the apparent complete absence of oögonia. Sections showed, in their stead in the cortex open sockets or cysts of all sizes from those barely

containing early germ-cells migrating inward from the germinal epithelium to those of partly grown follicles. These appear to be larger and more numerous posteriorly. They suggest a failure of germ-cells of female type to pass beyond the early stages of oögenesis before degenerating, perhaps from failure at synapsis or at some other stage of the growth phase. Posterior ones progressed further toward follicle-formation before succumbing (Figs. 18, 20, 24, 25, 26, 27).

The stroma is pigmented as in the normal hen-pheasant and in other "mule" gonads (Bissonnette, 1940). Primary and secondary sex-cords can be recognized in the medulla and in regions adjacent to the vacant cysts. In some places, particularly anteriorly, they contain tubules resembling those found in infantile testes, with cells resembling spermatogonia and partly activated Sertoli cells. They occur in all parts of the gonad, even farther forward than the vacant "oögonial sites" (Figs. 25-28). Regions resembling degenerated or cystic testis tubules also appear (Fig. 26). Lymphocytic infiltrations occur in the gonad and left epididymis like those in no. 3, but in fewer places (Figs. 20, 25, 26).

The histological picture suggests that, after the female germ-cells had developed to varying degrees they died off and degenerated into lipoidal cysts or vacuoles of various sizes from which the lipoids were leached out in the microscopical techniques of fixation and those leading to sectioning. Other germ-cells may have become spermatogonium-like and formed tubules of testicular type. This condition resembles that found in no. 2 "mule", but with fewer seminiferous tubules, and with vacant spaces for oögonia and follicles, not seen in no. 2. Loss of follicles may account for loss of female characters and for change over toward male plumage, very incomplete in this bird but more advanced in nos. 2 and 3. Paucity of testicular tissues and interstitials may account for the relatively slight development of male characters. The small size of the bird points to retarded development of the soma accompanying that of germinal tissue, resulting from some sort of incompatibility. No. 4 probably represents the earliest stage in a process of waning femaleness and waxing maleness among the four birds so far studied, with nos. 2 and 3 following in order of completeness of change-over.

Near the anterior end of the right adrenal and near a ganglion posterior to it, to the right of the abdominal aorta, were two or more nodules re-

sembling testicular tissue enclosed in a tunica propria. They are about 225 microns or less in diameter and are buried in the adrenal or in tissue adjacent to a ganglion medial to the epididymis. They may perhaps be clumps of aberrant adrenal tissue.

As shown in sections the left oviduct begins anteriorly as a pair of ridges on the ventral surface of the kidney posterior and lateral to the gonad (Fig. 29). A short distance caudally it flattens to a broad low ridge covered by a loose membrane formed by the peritoneum covering the kidney (Fig. 30). A groove then appears in its ventro-lateral margin, deepens, and is followed by a second groove in its medio-ventral margin. Both grooves deepen and their lateral walls elongate and converge toward each other over the grooves but fail to close ventrally to form a duct or tube (Figs. 31, 32, 33). The whole slit-like structure remains covered in by the peritoneum covering the kidney acting as a capsule in the form of a long narrow pocket. Posteriorly the flap-like sides of this oviducal groove thicken to resemble the floor in thickness and almost close in to form a duct (Fig. 33). It resembles an oviduct slit open lengthwise (Figs. 34, 35), and assumes the proportions and lining typical of an infantile oviduct, leads off from the kidney on a broad thin mesentery, the mesotubarium, while still retroperitoneal (Fig. 33). Much farther caudally the oviducal groove closes at about one-quarter of the way short of the edges of the margins of the flaps which form its sides (Fig. 36). It thus acquires a lumen but it still leaves a deep groove externally opposite to the mesotubarium (Figs. 36, 37). Much farther back this external groove or slit closes solidly and the inner surface of the duct changes and lands, and grooves appear in it (Figs. 38, 39). There remains a broad ligament or sheet of tissue extending ventrally from the surface of the oviduct opposite to the mesotubarium, and about as broad as half the diameter of the oviduct. This sheet gradually narrows and thins out so that the oviduct comes to resemble a normal infantile one posteriorly (Figs. 40, 41). The sheet or flap thickens again near the cloaca and contains some peculiar spongy tissue (Fig. 39). The whole structure exemplifies a very infantile and rudimentary oviduct, restricted to the left side.

DISCUSSION

The gonads of "mule" no. 3 show that, in some cases, the seminiferous tubules of the "ovary"

of the "mule" pheasant undergo active spermatogenesis during the breeding season. In this bird they were evidently activated to spermatogenesis early in the season, although no mature spermatozoa were evident at autopsy. There is strong probability that either earlier or later in the season spermatogenesis may reach completion. Sojourn of the bird for some days in a shady basement room before sacrifice may have induced some regression from complete activation. Pheasants are very susceptible to photoperiodic sexual stimulation (Bissonnette, 1939 and previous papers). The absence of matured sperm from these gonads need not preclude the possibility of previous complete spermatogenesis. Necropsy may have occurred during one of the periodically recurring waves of pressure degeneration which alternate with periods of activation of germ-cell elements, known to recur in testis grafts, after ligation of vasa efferentia, or in naturally occurring absence of vas deferens and epididymis (Pezard, Sand and Caridroit, 1924; Caridroit, 1926; Greenwood and Crew, 1926; Greenwood and Blyth, 1930; Moore, 1931). Differences in stages of activity or recovery in different parts of this "mule's" gonads lend support to this idea.

The change toward maleness of plumage with greater degree of male feathering in those "mules" with less ovarian or more testicular tissue strongly indicate a parallel change in these related structures, in line with Benoit's (1929) arrangement in series of physiological activations of secondary sexual characters. The presence of two oviducts in no. 3 "mule" and their type of enlargement and distention are due to enhanced production of male sex-hormone without the hyperplasia of their lining mucosa which would be induced by female hormone (Noble and Wurm, 1940). Such distention often appears in ovariectomized fowl and more rarely in those otherwise normal (Domm, 1932).

The development of both right and left gonad-rudiments of no. 3 into irregular ovary-like testes lacking ovarian follicles or eggs, but with greatly distended seminiferous tubules, is associated with the characteristically female loss of connections of mesonephric epididymal tubules from vas deferens to seminiferous tubules. Therefore gonad-rudiments of both sides may be affected simultaneously. Conditions in no. 4, on the contrary, show that sometimes the sex-gland and oviduct of only one side may develop accompanied by vasa deferentia and epididymides on

both sides. This probably depends upon the time and stage of development at which female differentiating factors begin to fail and male factors attain ascendance.

The failure of some tubules in no. 3 and of all in no. 4 to undergo activation to spermatogenesis, the presence of tubules in intermediate condition, and the spermatogenic activity of germ-cells in some sex-cords not yet organized into tubules, in no. 3, indicate that not all gonads nor all parts of the same gonad are equally susceptible to activation and that germ-cells need not be organized into tubules before being ready for spermatogenesis. There is also a suggestion that the seminiferous tubules in no. 4 may have been at too infantile a stage of development to respond to gonadotropins if they were present in normal quantity or potency.

In no. 3, the region of the left gonad nearest to the mid-line of the body was least activated, while almost, if not quite all of the right, usually rudimentary, gonad appears to have been susceptible to activation into spermatogenesis. This right one was shorter and narrower than the left. In no. 3 there is no question of unilaterality of the condition except for difference in size of gonads and oviducts. In no. 4, on the contrary, the primarily "female" sex-organs are unilateral, without recognizable remnants on the right side. "Male" ducts are bilateral in both "mules", as in normal pheasants of both sexes, and apparently bilaterally symmetrical in development and preservation.

In no. 3, the apparent dorsal distribution of the more female parts of the plumage from top of head to tail, including most of the wings, with maleness ventral, might suggest somatic non-disjunction as an accompanying anomaly. This, however, cannot be the cause for the persistence of two oviducts and gonads, not found in normal hen-pheasants. Evident lack of dominance of either male or female type of gonadal tissue or insufficient dominance of male tissue was not associated with arrested development of the soma in no. 3. It was in no. 4, which was evidently at a much earlier stage of the process of sex-reversal or female failure. This is attested by vacant places for oögonia, fewer testicular tubules, smaller, very rudimentary oviduct, failing to close anteriorly, less male feathering, and lack of spur development. It therefore exemplifies the earliest stage of such reversal with no. 2 intermediate and no. 3 farthest advanced of the three "mules" studied so far.

The single gonad of no. 4, very markedly, and those of no. 3, slightly, resemble those found in hybrids from wide crosses in Doves (Riddle and Johnson, 1939), in which a single small juvenile ovary is found, with shallow cortex, lacking oögonia in late stages of development, although these gonads may have had germ-cells earlier in the life of the birds. This condition was ascribed to an undescribed type of sex-reversal. Vacant spaces, left by disappearing oögonia or follicles, were not found in the Doves. The spaces found in no. 4 "Mule" seem to fit well with the theory of failure of female germ-cells at some phase of oögenesis and continued development of those of male type into seminiferous tubules. The apparent repression of the female sex in the Doves was ascribed to the wideness of the cross which in some cases led to gonadless birds. Conditions in these pheasant "mules" may also be due to hybridization. The Ring-neck pheasant is a hybrid between *Phasianus torquatus* and *P. colchicus* or *P. mongolicus* or all three. The number and frequency of these intersexes of sex-inverts among pheasants is much less than among the hybrid Doves described, but the crosses are not so wide.

Bullough (1940) has just described a somewhat similar change in some old female minnows (*Phoxinus laevis* L.) which appear to undergo sex-reversal to males in many respects. He concludes that the germ-cells in the female portion of the ovaries fail, the glands cease to secrete estrin, and testicular tissue makes its appearance and develops. The male hormone subsequently secreted causes final breakdown and elimination of ovarian tissue. This is followed by reversal of secondary sexual pigmentation. In our pheasants, failure of female elements occurred relatively early, in juvenile or early adult life, and male tissue took over to varying degrees, leading to apparent sex-reversal, or, perhaps more properly, to female failure and male usurpation of function following an original bisexual condition in which femaleness first predominated.

The disappearance of germ-cells or follicles in no. 4, leaving cyst-like cavities, indicates some incompatibility of cytological elements as the cause of failure of oögenesis during the growth phase and possibly at synapsis. This may be due to wideness or complexity of hybridization with alien male pronuclear substances failing to achieve compatibility in the cytoplasm of the maternal species at the critical period during synapsis. The time when this incompatibility

reaches a climax and factors for femaleness fail or lose control of differentiation and allow male differentiating factors to assume control, varies in different birds from different crosses of parent species. This resembles the type of reaction postulated by Goldschmidt (1931) for crosses between strong and weak races leading to intersexual females coming to exhibit male characteristics progressively later with weaker male strains in the cross or as the epistatic minimum for complete sex-expression falls short of realization.

It therefore appears that the "mule" pheasant is not due to the overpowering of an originally definite female sexuality by intervention of male hormone as in the cases of chicks from eggs injected with male hormone (Kozelka and Gallagher, 1934; Willier, Gallagher and Koch, 1937; and others cited by them) nor of sinistral ovariectomy allowing for temporary testicularization of the right gonadal rudiment (Benoit, 1923; Zawadowsky, 1926, Domm, 1927; and others). Those cases revert, in time, to their original genetic sex after transitory masculinization of plumage and other secondary sexual characters. The "mules" do not revert, so far as we know, but increase in amount of masculinization. They appear, therefore, to be due to inherent genetic weakness of female sex-differentiating factors which finally fail and permit hitherto almost repressed or masked inherent male differentiating factors and gonadal tissue to assume hormonal control of the soma, particularly the feathers, spurs, and head furnishings. The gonadal tissue itself becomes testicular and even undergoes seasonal breeding activity and spermatogenesis in some cases, perhaps not all.

Consideration of the above facts and generalizations of other workers may leave it still an open question whether this phenomenon should be regarded as sex-reversal or as intersexuality arising from incomplete dominance of female sex-differentiating factors in the sense of Goldschmidt. The soma appears to have been female in development up to various stages in different individuals in parallel with the gonads. Female factors appear to have lost their potency or run out and maleness and then male hormones to have assumed various degrees of control of further differentiation. It is concluded that the evidence favors a theory of intersexuality.

SUMMARY AND CONCLUSIONS

1. General feathering, gonads, and secondary sexual organs of two Ring-neck "mule" pheas-

ants, sacrificed for study during the breeding season in May and June are described. One, no. 3, is in the most advanced, the other, no. 4, in the earliest stage of change over from female to male sexual condition and plumage.

2. Both have bilaterally well developed epididymides and vasa deferentia ending blindly anteriorly, as do hen-pheasants.

3. No. 3 had many seminiferous tubules in both right and left ovary-like gonads, ending blindly without emptying into the epididymides, in different stages from infantile or resting winter tubules to distended ones with germ-cells undergoing spermatogenesis to spermatids, but no sperms. The tubules were probably in various stages of recovery from pressure degeneration, such as are found in other animals with exit of sperms blocked near the gonad.

4. No. 4 had but one "ovary" containing many cyst-like cavities suggesting that oögonia and small ovarian follicles had undergone lipoidal degeneration and been leached out by technical reagents, together with a few developing seminiferous tubules apparently too infantile to be activated by gonadotropic hormone in this, the breeding season, as those of no. 3 had been.

5. No. 3 had two unequal oviducts, the right the smaller, both in conditions indicating activation by male sex-hormone without female hormone effects, similar to that induced in castrate Night Herons by testosterone propionate or found in ovariectomized fowl.

6. No. 4 had but one oviduct very incomplete and rudimentary anteriorly, as a groove, and tubular and infantile posteriorly, showing no signs of male hormone activation as yet.

7. The findings suggest that these "mules" exemplify in pheasants various conditions of female intersexuality, in the sense of Goldschmidt, resulting from crossing species stronger or weaker in male and female sex-differentiating factors, with female differentiating factors failing in embryonic, juvenile, or early adult life. This leads to early or later development of maleness of plumage, spurs and head furnishings and to various conditions of gonads and secondary sexual apparatus.

8. The wideness of the crosses may be a factor in this unstable equilibrium, as it appears to be in gonadless and other intersexual hybrid Doves.

9. No. 3 "mule" may have somatic non-disjunction as an added factor leading to dorsal distribution of female and ventral distribution of male feathering.

10. The active spermatogenesis, producing spermatids, in the testis tubules of no. 3 "mule" demonstrates that these intersexual gonads are responsive to the cycle of gonadotropic hormone production with the seasons, when not too infantile, and become active in the breeding season.

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PLATE I

FIG. 1. Left side of "Mule" Pheasant, no. 3, to show ring-neck and dorsal distribution of "female" feathers and ventral "male" feathering.

FIG. 2. Right side of "Mule" Pheasant, no. 3, as above.

FIG. 3. Ventral view of "Mule" Pheasant, no. 3.

FIG. 4. Ventral view of "Mule" Pheasant, no. 3, to show red ring around the eye and male ventral feathering.

FIG. 5. Dorsal view of "Mule" Pheasant, no. 3, to show female feathering.

FIG. 6. Photographs of legs of "Mule," no. 2 or 4, normal female, and "Mule," no. 3, to show relative spur development.

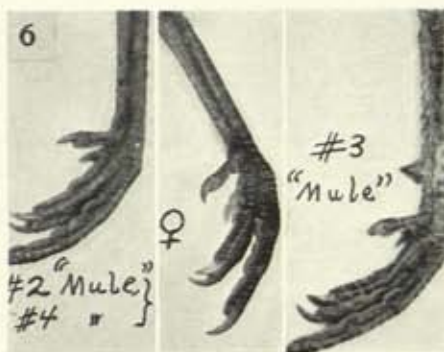
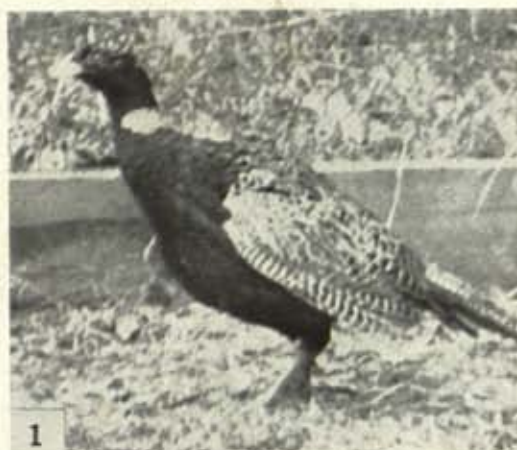


PLATE I

PLATE II

FIG. 7. Side view of head and neck of "Mule" Pheasant, no. 4, to show ring-neck, red area around eye, and denuded skull.

FIG. 8. Dorsal view of head and neck of "Mule" Pheasant, no. 4, to show denuded bare dry skull and granulation zone around it, and dorsal part of white ring on neck.

FIG. 9. Photograph of ventral view of reproductive system of "Mule" Pheasant, no. 3, showing two oviducts, right and left gonads lobulated like ovaries and their relations to the kidneys.



PLATE II

PLATE III

FIG. 10. Photomicrograph of cross-section of anterior end of left gonad (or "Mule," no. 3) to show seminiferous tubules, cortex and medulla of "ovary," pigmentation, and lymphocytic infiltrations. $\times 34$.

FIG. 10a. Cross-section of left gonad about its middle. Shows epididymis in lower right corner with lymphocytic invasion. $\times 34$.

FIG. 11. Cross-section of left gonad showing various conditions of spermatogenesis in blind tubules. $\times 84$.

FIG. 11a. Another section of left gonad of "Mule" Pheasant, no. 3. $\times 84$.

FIG. 12. Section of right gonad with epididymis in lower left corner. $\times 34$.

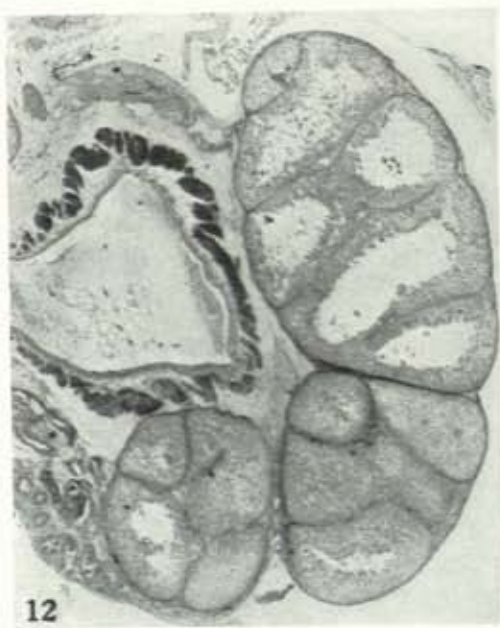


PLATE III

PLATE IV

FIG. 12a. Section of right gonad; seminiferous tubules. $\times 335$.

FIG. 13. Section of right gonad. $\times 84$.

FIG. 13a. Section of an interstitial region and adjacent tubules of right gonad enlarged from Fig. 13. $\times 335$.

FIG. 14. Cross-section of left gonad to show large cyst-like region, probably a degenerate seminiferous tubule, and active seminiferous tubules in various stages of spermatogenesis. $\times 34$.

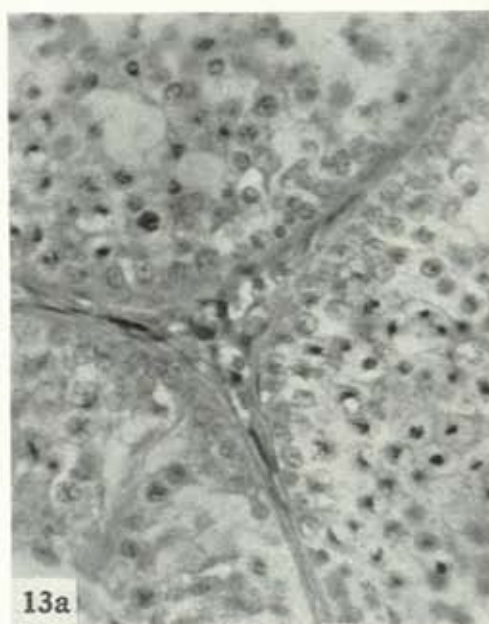
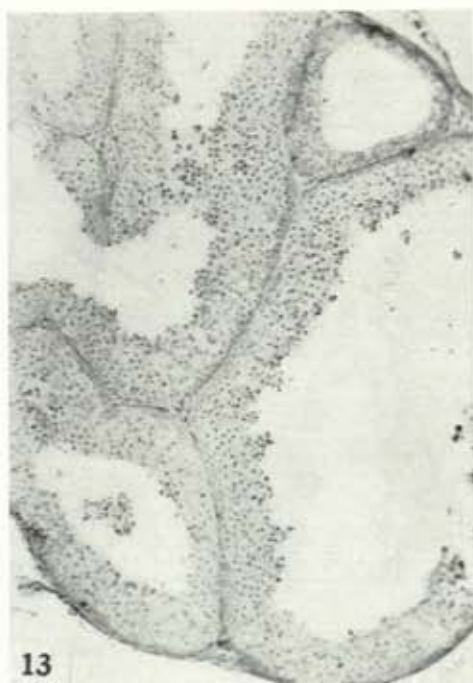
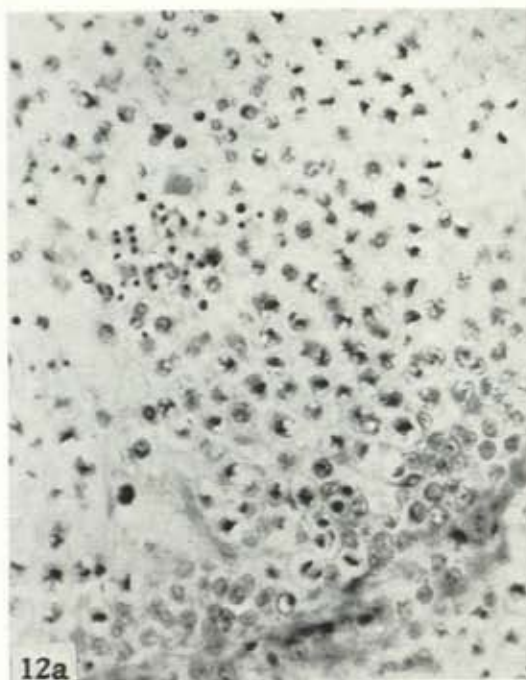


PLATE IV

PLATE V

FIG. 15. Section of Fig. 14, enlarged to $\times 84$, Part of cyst-like region and adjacent active tubules.

FIG. 16. Section of cyst-like region and active tubule of left gonad. $\times 335$.

FIG. 17. Cross-section of typical left oviduct of "Mule" Pheasant, no. 3. $\times 34$.

FIG. 18. Cross-section of left gonad and epididymis of "Mule" Pheasant, no. 4, to show vacancies where follicles have apparently been eliminated, some seminiferous tubules in infantile condition and pigmented medulla and cortex. $\times 84$.

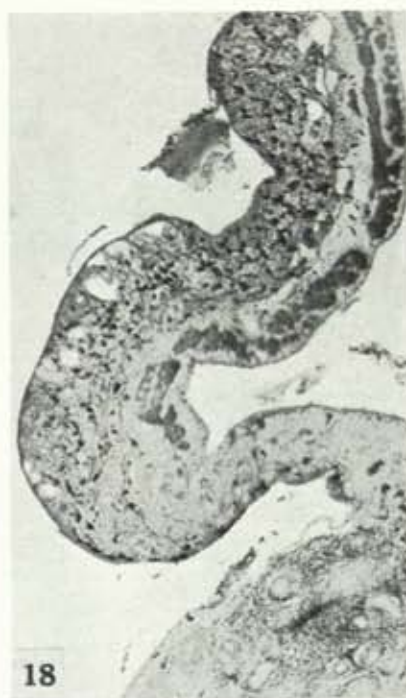
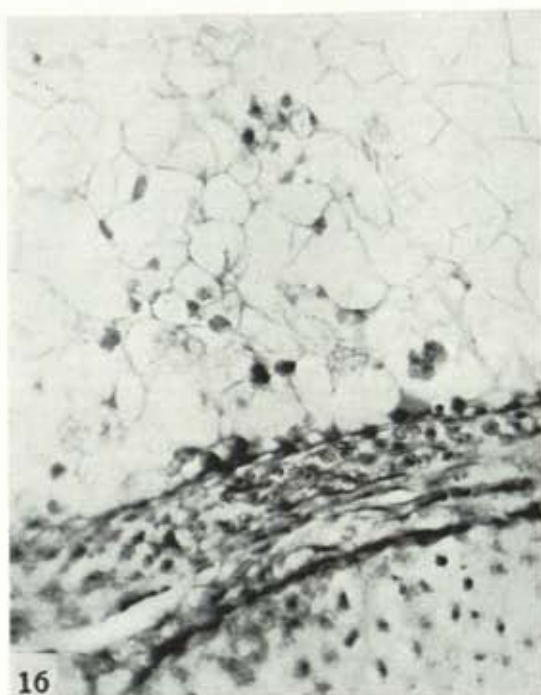
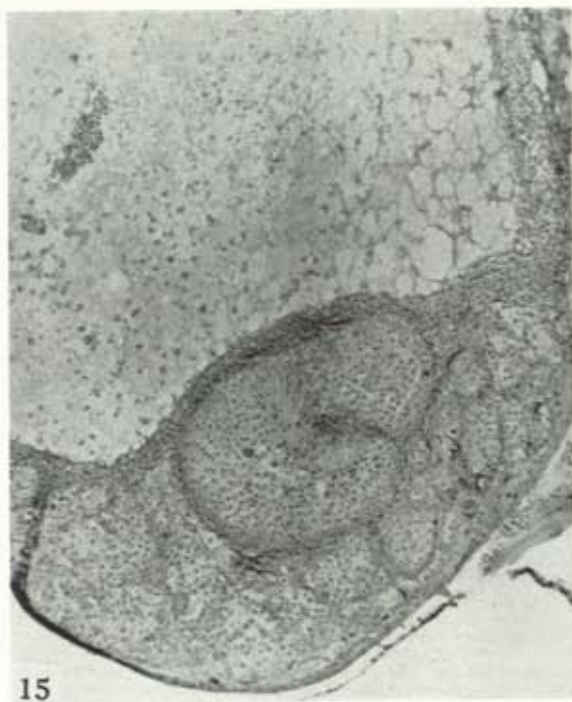


PLATE V

PLATE VI

FIG. 19. Cross-section of left epididymal tubules to show colloid in some tubules and others vacant. $\times 335$.

FIG. 20. Cross-section of left gonad and epididymis of "Mule," no. 4, near the posterior end of the gonad to show some tubules in the epididymis similar to those in the gonad and some fairly typical epididymal tubules. $\times 84$.

FIG. 21. Cross-section of right epididymis at same level as Fig. 22. $\times 84$.

FIG. 22. Cross-section of left epididymis of "Mule," no. 4, at the same level as Fig. 21 for right one. $\times 84$.

FIG. 23. Cross-section of left epididymis of "Mule," no. 4, to show tubules in it like those in the gonad among normal epididymal tubules. $\times 84$.

FIG. 24. Cross-section of left gonad of "Mule," no. 4, folded on itself. Shows large vacant spaces or cysts where ovarian follicles or oögonia have apparently been eliminated. $\times 84$.

FIG. 25. Cross-section of left gonad of "Mule," no. 4, showing vacant "follicles" and infantile seminiferous tubules. $\times 84$.

FIG. 26. Another section of left gonad to show other regions containing similar "follicles" and tubules. $\times 84$.

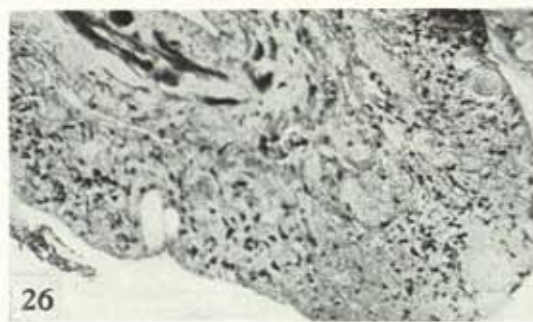
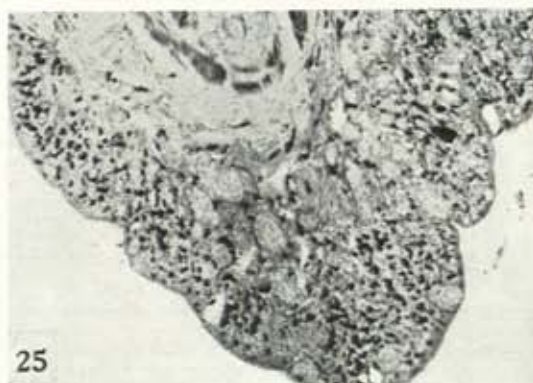
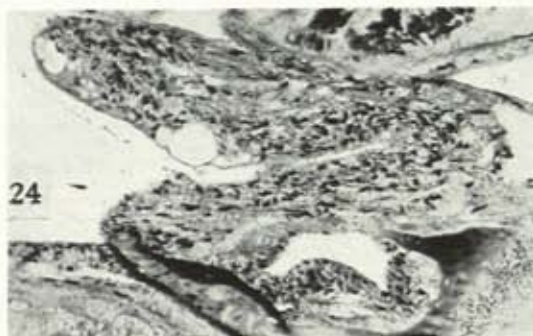
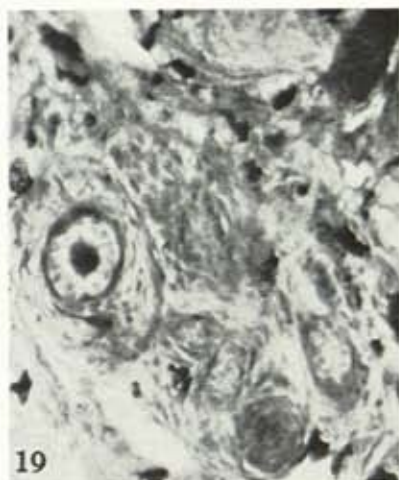


PLATE VI

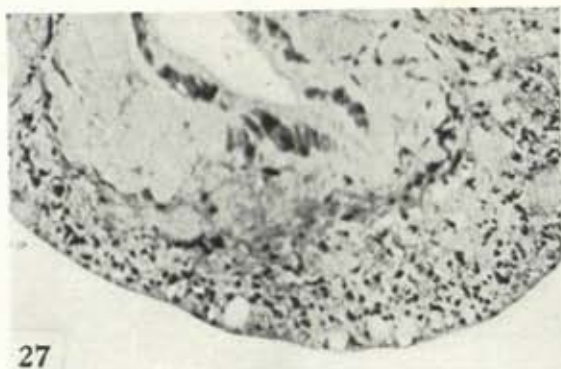
PLATE VII

FIG. 27. Cross-section near posterior end of gonad of "Mule," no. 4, showing one or two tubules and several vacant "follicles". $\times 84$.

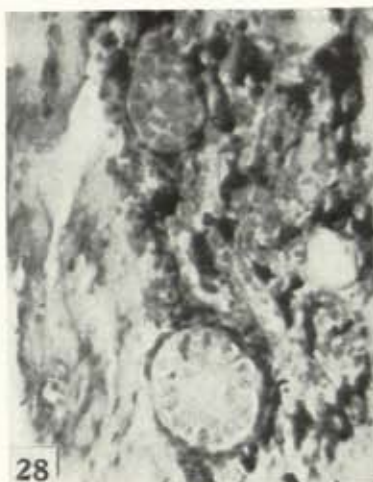
FIG. 28. Region of gonad of "Mule," no. 4, with two seminiferous tubules containing sertoli-like cells and cells that resemble spermatogonia. $\times 335$.

FIGS. 29, 30, 31, 32, 33. Sections of the anterior end and region of the oviduct of "Mule," no. 4, in order antero-posteriorly. $\times 84$.

FIGS. 34, 35, 36, 37. Succeeding cross-sections through the oviduct to show closure leaving two flaps and ventral groove and change in type of lining as sections are farther posteriorly. $\times 34$.



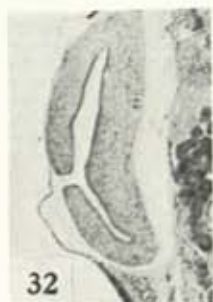
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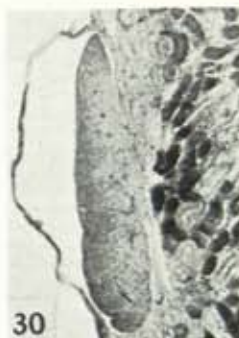
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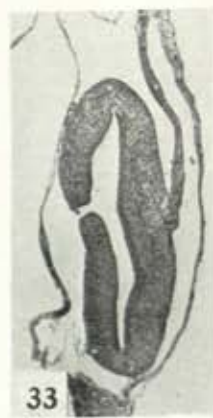
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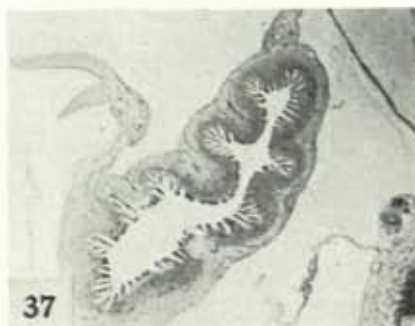
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31



34



37



SOME PRE-ARMADA PROPAGANDIST POETRY IN ENGLAND (1585-1586)

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(Read April 26, 1941)

ABSTRACT

In the years 1585 and 1586, when England was expecting invasion by Spain, and combating "fifth-column" activities which centred around Mary Queen of Scots, the Oxford University Press issued a series of sixteen-page pamphlets intended to sustain the national morale. They were in Latin verse and appear to have had a wide distribution, but they have never been reprinted and are almost unknown to bibliographers. A set has been discovered at the Huntington Library and another at Winchester College, England. The most interesting of the contents are twelve odes, written during 1585 and 1586 and offering practically a month-by-month expression of national feeling.

THE year 1584 was one of great national apprehension in England. The Prince of Orange was assassinated on July 10 by a Jesuit agent, and similar plots against Queen Elizabeth that were being discovered in likely and unlikely places threw the country into a fury of excitement over what would now be called "fifth-column" activities. The Earl of Leicester, Chancellor of Oxford University, took the lead in forming the "bond of association" and in laying plans which culminated in the famous parliamentary act of November 23, "for the security of the Queen's person and continuance of the realm in peace".

In August, 1584, the University of Oxford directed that one hundred pounds be allowed to Joseph Barnes, a bookseller, in order that they might have a press in the University, and this was the real beginning of the Oxford University Press. Among the earliest, and today quite the rarest, of its publications is a series of sixteen-page pamphlets, issued in 1586 and 1587, and evidently intended to maintain the national morale. As befitted a learned press, they are in Latin, and in Latin verse of admirable quality. The first two, dated 1585, deal with the case of Dr. William Parry, who was executed as a traitor on March 2 of that year. One, entitled *Pareus*, treats the matter epically in hexameter. The other, *In Guil. Parry proditorem odæ & epigrammata*, consists of separate poems. The three Horatian odes, from the pen of William Gager of Christ Church, the most accomplished Latin poet of this age, occupy six pages, and the

rest are filled by a series of epigrams in elegiac verse against Parry, the Anglo-Romans, and the Pope.

The next year, 1586, brought more plots to kill the queen and more Horatian odes by Gager on the subject. Six of these, different from the three on Parry that had been printed the previous year, were published, again in a sixteen-page sheet, with the title, *In Catilinaris proditones*. A wide sale was apparently expected, for the imprint notes that copies can be purchased in London, at the sign of the Tiger's Head in Paul's Churchyard.

The first is an impassioned malediction upon the evil days in which Gager is living. He would like to be borne beyond the Pillars of Hercules to the new world that Drake has visited, for the old world breeds traitors hydra-like, and the ancient British virtue has been polluted by Italian guile. He asks (if I may be permitted to rime his Latin):

When will the headsman leave his work,
And cleanse the stain of felon gore?
When shall I see the axe at rest,
And in the Tower no prisoners more?

The second ode is addressed to the most recently discovered of the Catholic plots, by which the navy and the city of London were to be set on fire. The poet has a vision of the queen sorely wounded and Britain scourged with flame and rapine. In the third ode he turns from the Alcaic stanza in which all the rest of this series are composed, to express in Sapphics his exultation at the queen's escape; and in the fourth he dilates upon the usual failure of treasonable plots and the miseries of a traitor's life. In Ode 5 he enforces with characteristic Old Testament instances the truth that regicide is the most impious of crimes; and in the sixth he urges the queen to have no mercy on traitors, pitiable as were the cases, he admits, of Tichborne and Salisbury, who were executed in September of this year. He incites Elizabeth to a supreme effort, like that of Jupiter against the rebellious Titans, and closes with impressive prophecy:

IN CATILINARIAS PRODI- TIONES, AC PRODI- TORES DOMESTICOS, Ode 6.



OXONIÆ, ex Officina Typographica IOSEPHI
BARNESII, & venient in Cameræ Paderb.
sub signo capitis Tygrii. Anno 1586.

No poison, Queen, shall take you off,
No guile, revolt, or dagger stroke.
You'll gently pass, when ripe for fate:
Believe this, as if the Sibyl spoke.

Such work cannot but have been popular, and it is natural that a new issue of the odes was required before the year was out. By that time Gager had written three others, following the development of events, and these were squeezed within the limits of a sixteen-page pamphlet by printing the title on a separate leaf and beginning the text on signature A1 instead of A3.

The seventh ode is a sonorous vindication of the queen's character, and here for the first time Gager makes undoubted reference to Mary of Scotland, asking concerning his own queen,

When has *she* foully slain her mate?
Or when eloped? Not *hers* the guilt
Of wedlock fit for tragic stage,
And blood of folk and nobles spilt!

The next ode is addressed to the kings of Christendom, warning them in their own interests to destroy the English traitors who have found refuge in their realms; and the ninth brings the series to a fitting conclusion. It looks to the coming of the Armada, and appeals to Englishmen of every party to love their country and unite in resistance of all foreign domination.

The series of publications to which these odes of Gager belong has suffered the too usual fate of unbound, ephemeral literature. They have almost disappeared from the earth and have eluded the search even of the historians of the Oxford Press. Two sets of them, however, exist, bound up with other works. One passed through the hands of Richard Triplett, whose signature appears on the reproduced title-page, and who matriculated from Trinity College, Oxford in 1687, aged sixteen. It contains both the six-ode and the nine-ode edition of the poems printed below, and is now in the library of Winchester College, England. I am indebted to the Warden and Fellows of that School for permission to reproduce them and to the Librarian, Mr. C. E. R.

IN CATILINARIAS PRO- DITIONES, AC PRO- DITORES DOMESTICOS, Ode 9.



OXONIÆ, ex Officina Typographica IO-
SEPHI BARNESII, Anno 1586.

Clarabut, for much courteous assistance. The other set, containing the nine-ode edition only, is in the Henry E. Huntington Library, to whose officers I must once more avow my gratitude. There are no important textual differences between the copies, though the later edition has been entirely reset.

ODAE 9,
ORNATISSI-
MIS VIRIS D. DO-
CTORI IAMESO, AE-
DIS CHRISTI OXON. DE-
CANO, ET D. DOCTORI HE-
TONO PRODECANO, CAETERIS-
QUE CLARISSIMIS ATQUE OP-
TIMIS VIRIS EIUSDEM EC-
CLESIAE PRAEBENDARI-
IS, ET PRIVATAE OB-
SERVANTIAE, ET
PUBLICAE PIE-
TATIS ERGO,
DICATAE.

In Domesticas, & immanes nostrorum
hominum ac temporum proditioes,

ODE PRIMA

Nunc est per auras cum libet hinc rapi
Quacunque turbo praecipitem vehat,
Alcidis ultra vel columnas,
Magnanimosue Draci labores.

Nunc est sub antro quando libet tegi,
Ipsisque vitam degere cum feris,
Et glande vescentem caduca
Innocuis latitare Syluis.

ODE 1

Against the monstrous internal treasons of our
citizens and times.

Now is a time when I wish to be snatched hence through
the air, whithersoever the whirlwind can blow me head-
long, past the Columns of Hercules or the daring voyages
of Drake.

Now is a time when I wish to be shrouded in a cave
and pass my life with the very beasts, to hide in the
inoffensive woods and feed on the fallen acorn;

Quo Proditoris nulla domestici
Pertingat unquam fama, ubi perfidus,
Laesaeque maiestatis unquam
Nemo mihi reus audiatur.

Quae dira, credam, toxica moribus
Aspersa nostris? tempora quae putem?
Quae terra? quae gens? quae libido
Non nisi grande nefas patrandi?

Faecunda culpa nostra quot edidit
Aetas Cethegos? quot modo Lentulos?
Iam creber urbi, Consulique
Insidias Catilina tendit.

Monstrumque maius, crimina pullulant
Dum puniuntur: iamque oritur scelus
Non unum in uno, sed resecta
Proditio, velut Hydra, crescit.

Ecquando ponet vincula carnifex?
Sontisque tabem sanguinis abluet?
Ecquando securas secures
Aspiciam, vacuumque Turrim?

O Christiani infamia seculi
Contracta nuper! pro scelus, et nefas
Non iam Britannis, sed vel ipsis
Turcigenis etiam pudendum.

Where no news of the domestic traitor, can penetrate,
where no disloyal person, and no man guilty of treason can
ever be heard of by me.

What fatal poisons shall I believe instilled in our con-
sciences? What times shall I think these to be? What
an earth, what a race, what a passion for the accomplishing
of nought but hideous crime!

How many Cethegi and Lentuli this sinful age of ours
has lately produced! Not one Catiline, but many now
spread their snares for the city and the chief magistrate.

And a greater horror: crimes propagate even while they
are being punished; and now sin does not come singly in
the single sinner, but treason grows like the hydra even
as it is cropped.

O when will the executioner impose restraint, and wipe
away the pollution of guilty blood? When shall I see the
axes unemployed, and the Tower free of prisoners?

O newly devised infamy of this Christian age! Ah crime
and sin, shameful now not merely to Britons, but even
to the Turks themselves!

Nostri quis orbis, vel Tagus eluet
 Nilusue tantam, vel Thamesis notam?
 Non ipse qui cingit Britannos
 Caeruleus pater expiarit.

Collecta, per tot secula, criminum
 In nos redundat sarcina, perditæo
 AEuo grauemur, quo malorum
 Omne genus, scelerumque regnat.

Non his, iuuentus incluta, moribus
 Regno ferocem adiecit Hyberniam,
 Gallumque et Hispanum fugavit
 Non semel, indomitumque Scotum.

At nostra turpi dedita luxui,
 Fortisque solum virginis in necem,
 Artes dolosas tractat, ex quo
 Italico medicata fuco est.

In horribilem, & plane Catilinariam
 coniurationem nouissime factam,

ODE 2

Ergone si quid fraus poterat mala,
 Extinctam Elisam lugubris Anglia
 Iam fletet? arderentque naues?
 Iam patriam cinis occuparet?

What Tagus, or Nile, or Thames will wash out this stain
 of our world? Not even the dark blue ocean-father who
 encircles us Britons could make us clean.

The weight of crime, heaped up through so many genera-
 tions, pours upon us; we are weighed down by a desperate
 age in which every kind of evil and of sin is dominant.

It was with no such ideals as these that our splendid
 youth united fierce Ireland to our kingdom, and more
 than once put to flight the Gaul and Spaniard and the
 indomitable Scot.

But our youth of to-day, abandoned to base excess and
 bold only for the slaughter of a virgin, practices deceitful
 arts, from the time that it is besprinkled with Italian guile.

ODE 2

Against the horrible and quite Catilinarian conspiracy
 most recently perpetrated.

So, if wicked guile had its effect, distressed England would
 now be weeping for the slain Eliza, and our ships would
 be burning, and our fatherland reduced to ashes?

O impiorum viscera barbaro
 Obducta ferro! posteritas fidem
 Facti negabit, vix vel aetas
 Nostra putet scelus institutum.

Regina tantum quid meruit pia?
 Regina miti Candida pectore,
 Diuina virgo, qua recurrens
 Nil melius videt orbe Titan.

Non illa vobis, dira lues, placet:
 Ast illa nobis perplacet, et Deo,
 Sanaeque plebi, quam tuentur
 Tot Procerum, populique vota.

Vos terra Diris prosequitur pijs,
 Poscitque poenas immiserabiles;
 Odere ciues, virginumque
 Casta cohors scelus execratur.

Vix dum ipse tantos deposui metus;
 Totus stupesco, membra quatit tremor,
 Cum destinati saeua mentem
 Forma mali subit, atque imago.

Detestor omen; sed video tamen
 Crudeli Elisam vulnere sauciam,
 Pulchros per artus ire cerno
 Virginei lateris cruorem.

O bowels of sinners, covered with barbaric iron! posterity
 will refuse credence of your deed; hardly can even our age
 believe the crime you have purposed.

How has our noble queen deserved all this? Our queen so
 radiant with her tender heart, a heavenly virgin, than
 whom the circling sun sees nothing better in his course?

To you, ye deadly plague [of traitors] she is displeasing;
 but us she pleases much, and God, and her sound-hearted
 commons, and the manifold loyalties of her nobles and
 people protect her.

The earth pursues you with righteous portents and
 demands pitiless punishment; the citizens hate and the
 chaste band of virgins abhor your crime.

I myself have hardly yet thrown off these great alarms;
 I am all confounded, trembling shakes my limbs, when
 the horrid shape and idea of the plotted mischief comes
 into my mind.

I deprecate the omen; but yet I see Eliza smitten with a
 cruel wound, I behold the blood of her virginal breast
 flowing down her beautiful limbs.

Collapsa ceruix in niueos sinus
Laxe recumbit: sic ubi lilia
Succisa languescunt aratro,
Aut pluuiæ grauidum papauer.

Flagrare classem cerno Britannicam,
Urbes cremari, faemineos rapi
Artus capillo, virginesque
Et iuuenes trepidare inermes.

Quo tam impotenti Musa ruis pede?
Ah siste: res hæc digna Philippicis,
Aut asperi diris Iambis
Archilochi, aut Senecæ cothurno.

In Serenissimam Reginam Elizabetham ex
imminente capitis periculo ereptam,

ODE 3

Quis mihi centum Deus ora, centum
Quis dabit linguas, totidemque voces
Ferreas, plenæ pia quæ refundant
Gaudia mentis?

Musa, dic cantus, age, seculares,
Carmen in Festo mihi seculari
Prome, quod longum, Dea, seculari
Viuat honore.

Her strengthless neck lies inertly upon her snowy bosom,
just as where lilies languish when cut off by the plough
or the poppy bent down with rain.

I behold the English fleet in flames, the cities burning,
women dragged by the hair, and the helpless girls and
boys in a panic.

Whither, Muse, are you rushing on such powerless feet?
Ah, pause. This matter is worthy of Philipps, or the
boding iambs of harsh Archilochus, or the buskin of
Seneca.

ODE 3

Upon the most serene Queen Elizabeth, rescued from
imminent peril of her life.

What god will give me a hundred mouths, a hundred
tongues, and as many voices of iron, to pour out the
loyal joys with which my mind is overflowing?

Come, Muse, recite songs for the ages; produce me on
this historic festival, a poem which may live long in
age-old honour.

Quo rapis Cleio? videor repente
Iam super Pindo, gelidæ in Haemo,
Iamque Parnassi placido vagari
Vertice montis.

Ecce, quæ cerno, loca grata, Tempe?
Quasque per ripas eo, quos per amnes?
Quis Caballini mea labra fontis
Proluit unda?

Proluor; nam quæ mihi mens canendi,
Quis furor venit nouus, unde tantus
Ardor inuasit? libet incitatum
Fundere carmen.

Daulias non me Philomela cantu
Non olor vincet, licet illa tristes
Defleat casus, licet ille iam sit
Iam moriturus.

Versibus non me superet Catullus,
Nec lyra Flaccus, licet ille doctus,
Hic licet præstet Lyricis, et astra
Vertice tangat.

Quid moror? non me superabit Orpheus
Thracius, quamuis pater huic Apollo,
Nec Linus, quamuis Dea mater illi
Calliopea.

Whither are you taking me, Clio? Suddenly I now seem
above Pindus, or on frosty Haemus, and now to be wander-
ing on the quiet top of Mount Parnassus.

Lo, Tempe, what lovely landscapes I behold! and along
what banks I go, beside what rivers! Who is it that
washes my lips with water from the fount of Hippocrene?

I am washed clean; for what an urge to singing, what
new mad impulse has come over me! Whence has so great
a passion entered me? It is a joy to pour forth the
rapid melody.

Neither the Phocian Philomela nor the swan shall surpass
me in song, even though the one be bewailing her sad
misfortunes and the other be on the point of death.

Catullus shall not excel me in versifying, nor Horace
on the lyre, though the former is cunning, though the
latter is preëminent among lyrists and touches the stars
with his brow.

Why delay I? Thracian Orpheus shall not exceed me,
though Apollo was his father, nor Linus, though his
mother was the goddess Calliope.

Sospes exstructo (memorare dulce est
 Quod pati durum nimis ah fuisset)
 Sospes erepta est quasi fax Elisa
 Nuper ab igne.

Quam malignorum prope funerarat
 Turba periuris scelerata dextris,
 Ni Deus tutam medios per enses
 Eripuisset.

Ergo si remo mare defatigans
 Seruus Hispano, medijsue Turcis
 Degerem infaelix, Libycisue nudus
 Syrtibus exul,

Annuos laeto tamen ore cantus
 Funderem, ad remi modulantis ictum,
 Muneris tanti memor, exararem
 Carmen arena.

Iamque vix memet capio, libetque
 Eloqui, mens est ululare syluis
 Maenadum ritu, iuuat, et decorum est
 Ire per antra.

Efferor; quid si minus appropinquet
 Auribus diuae mea vox Elisae?
 Audient colles tamen, et sonabunt
 Undique rura.

Safe from the heaped up pyre—(how sweet to remember
 what [had it chanced otherwise] would have been too
 hard to endure!)—safe is Eliza, lately snatched like a
 brand from the burning.

Whom the impious band of malignants had nearly de-
 stroyed with their traitorous hands, had God not borne her
 safe from amid their swords.

Therefore, if I should live to be a galley-slave to the
 Spaniard, wearying the sea with my oar, or an unhappy
 captive among the Turks, or a naked exile on the Libyan
 shoals,

Yet with a happy voice I should pour forth my songs
 each year as the beat of my oar kept time, in memory
 of so rich a blessing, or should write out my poem in
 the sand.

And now I hardly can contain myself and have a joy in
 speaking out; my will is to shout in the forests after the
 fashion of the Bacchantes; it is pleasant and fitting to
 dance through the grottoes.

I am carried away. What though my voice can hardly
 reach the ears of the divine Eliza? Yet the hills shall hear,
 and the solitudes reecho on every side.

Voce campanas superabo septem,
 Audiet longe, mediumque sese
 Rumpet Hispanus, veluti solutus
 Carmine serpens.

Audient dumi; neque vel leaenae
 Vel lupi occursum metuam, vel apri,
 Dum cano laetus nece liberatam
 Elisabetham.

Me tegat mundi plaga inhospitalis,
 Seu gelu squallens, nimioque sole,
 Dulce erit saluae meminisse Elisae
 Dulce referre.

Proditorum nefarios conatus
 plerumque irritos esse,

ODE 4

Quo Proditorum stulta ruit cohors?
 Quid spes inanes pascit, et impias?
 Quid nectit occultos furores?
 Et vacuas meditatur iras?

Ecquando vanos sentiet exitus,
 Tristesque casus, illachrymabili
 Fato trahentes se, domumque
 Et proavos, sobolemque nequam?

My voice shall have more power than seven bells; far
 off the Spaniard shall hear it and burst amidst ships, like
 a serpent destroyed by a spell.

The thorn-bushes shall hear, and I shall fear to meet
 neither lioness nor wolf nor boar while happily I sing
 of Elizabeth saved from death.

Though some inhospitable zone of the world enclose me,
 hardened with ice or with excessive sun, it will be sweet
 to remember that Eliza is safe, sweet to repeat it.

ODE 4

That traitors' nefarious attempts
 are commonly ineffectual.

Whither is the stupid congregation of traitors hastening?
 Why does it feed idle and impious hopes? Why does it
 weave secret furies and entertain empty rages?

When will it realize its vain results and doleful over-
 throws, which bring to unpitied ruin itself, its house and
 ancestors and worthless offspring?

Namque ut reuulsam seditionibus
 Deleret urbem Gallus, et insolens
 Hispanus, authores ad ipsos
 Quanta mali quoque pars rediret?

Delectet hostem proditio, tamen
 Quis Proditorem diligit, aut fide
 Credat secunda, ex quo fefellit
 Prima Deum, patriam, et penates?

Suspectus ergo turpiter exigit
 Vitam, acriorem morte, sibi grauis,
 Et seculi crimen, Deique
 Ira furens, hominumque pestis.

Quid quod rebellem turris ahenea
 Ut cingat, et nox vel pice nigrior
 Occultet insanos tumultus,
 Ante diem facinus patebit?

Claudat fenestras impius, et fores
 Obducatur intus mille, tegat leues
 Rimas, recessu Dedalaeo
 Implicitum Labyrinthus abdat:

Postes loquentur consilium tamen,
 Eliminabit ianua, garrient
 Ipsae volucres, et susurros
 Ambiguos pia musca sparget.

For though the Gaul and haughty Spaniard should destroy
 our mutinous city, what a large part of the disaster would
 come home to the authors themselves!

Treason may please the enemy, but who can love the
 traitor or trust in a second fealty from one whose first has
 betrayed his God, his country, and his household?

Distrusted, therefore, let him in shame lead a life bitterer
 than death, a burden to himself and a blot on his age,
 the maddening wrath of God and plague of men.

Moreover, though a brazen tower surround the rebel,
 and a night blacker than even pitch conceal his mad
 revolts, before day his offence will lie revealed.

Let the offender close his windows, and lock himself
 within a thousand doors, let him cover the tiny cracks, and
 let a labyrinth conceal him, sequestered in a Daedalian
 maze:

Nevertheless, the door-posts will proclaim his secret,
 the gateway will blab it, the very birds will talk, and
 the dutiful fly will spread abroad dark whisperings.

Ne crede syluis, cum scelus apparas,
 Aurita sylua est: ne domui tuae,
 Muris ocelli insunt, domusque
 Tota nefas videt, et recludet.

Ut nemo prodatur: ne tibi, ne tuae
 Confide menti: saepe tremens timor,
 Horrorque vultus, saepe pallor,
 Saepe stupor scelus occupauit.

Ut tute celes: quae tamen exedent
 Curae, quis angor pectoris, et minae
 Insomniorum? hic crede Manes,
 Et triplices habitare Diras.

Omnem expauescit Proditor ad sonum,
 Horret susurros, omnia dum putat
 De se referri, seque nullo
 Propriet pede persequente.

Collum ille zona, pensilis a trabe,
 Recte sequuta fregit, eum furor
 Torsit, venenum absorpsit alter,
 Hic proprio latus hausit ense.

Si cogitati tanta animum grauet,
 Quae deprehensi est sarcina criminis?
 At perpetrati quanta poena est?
 Qui stimuli, furiaeque pungunt?

Put no faith in the forests when you plot a crime; the
 forest has quick ears: nor in your house; the walls have
 eyes, and the whole house witnesses your sin and will
 disclose it.

Though no one betray you, trust not yourself or your
 own mind: often tremulous fright and an agitated coun-
 tenance, often paleness, often obsession, have betrayed sin.

Though you conceal it safely, yet what anxieties will con-
 sume you, what torment of soul and terrifying dreams?
 Believe me, here dwell the infernal ghosts and the three-
 fold Furies.

At every sound the traitor trembles; he is aghast at
 whispers, thinking everything to have reference to himself,
 and he will flee away when no foot pursueth.

Dangling from a beam one has broken his neck with well
 employed girdle, madness has racked another, one has
 drunk poison, and another lanced his breast with his
 own sword.

If such a burden oppresses the mind for the meditated
 crime, what is the burden of the crime detected! And
 what the penalty for the crime committed! What goads
 and furies pierce the doer!

Ultor rebellem persequitur Deus,
Et cogitatos deserit exitus,
Ridetque fraudes, et nefando
Supplicium capiti reservat.

In Proditores, summeque impium facinus esse
Principi violentas manus inferre,

ODE 5

Quisquamne credat? relligio nefas
Immane velat; tollere Principem
Coelo beatur, resque sancta est;
Grande scelus, pietas vocatur.

Hoc crimini unum defuerat, Deum
Facto aduocari: desine Proditor
Et numen insons inquinare,
Et Superos onerare probris.

Saulemne Daudid prodidit impium,
Iam certus haeres? quid simile est tamen?
Nec Saul Elisa est, nec, futuro
Vos geritis pia bella, Regi.

Is nescienti grande nefas putat
Scidisse vestem: vix cyathum manu
Hastamque tollit; vos Elisae
Et vigili, caput auferetis?

An avenging God pursues the rebel and turns his back
upon his plotted ends, laughs at his wiles, and lays up
punishment for his execrable head.

ODE 5

Against Traitors, and that the most impious of crimes
is to lay violent hands upon a prince.

Can anyone believe it? Religion cloaks heinous crime!
Regicide is blessed by heaven, and is a holy thing! enormous
sin is called piety!

This alone was wanting to crime: that God should be made
advocate of the deed! Cease, Traitor, to besmirch inno-
cent divinity and load the higher powers with your sins.

Did David, now unquestioned heir, betray wicked Saul?
What is there like in that? Neither is Saul Elizabeth, nor
are you waging pious wars for the king to be.

David thinks it a great wrong to have cut off the skirt
of Saul's robe privily, he hardly takes with his hand the
cruse of water and the spear. Will you take off Elizabeth's
head, even when she is on guard?

Is fata Saulis tristitia flet pius,
Et nuntiantem morte remunerat,
Vel mentientem; vos Elisam
Fletis adhuc superesse terris?

Certe tyrannum, vel citus auferet
Morbus, vel ensis, quem patitur Deus
Nos ferre par est, et piorum
Arma, preces lachrymaeque sunt.

At Sheba Regem pessimus optimum
Conatur armis tollere subditis:
Daudis ergo est non ferire,
Degeneris fera dextra Shebae est.

Ad Serenissimam Reginam Elizabetham, ne
Proditoribus parcat, eiusque salutem
Deo charam esse,

ODE 6

O Patre forti filia fortior,
Et matre pulchra filia pulchrior,
Regina, nostrarumque robur
Post Superos, columenque rerum:

Dic diua virgo, mens tibi quae fuit?
Vultus serenos quis subiit color,
Cum Proditorum prima nuper
Fama tuas violaret aures?

Godly David laments the sad fate of Saul, and rewards with
death the announcer of it, even though a liar. Do you
lament that Eliza is still present on the earth?

Certainly either quick disease or the sword will rid away
the tyrant. [The ruler] whom God suffers, it is right
for us to bear, and the arms of the righteous should be,
[merely] prayers and tears.

But a most wicked Sheba attempts to remove the best
of kings by subject arms. Therefore, it is not for a
David to strike; the hand of violence is the hand of de-
generate Sheba.

ODE 6

To the most serene Queen Elizabeth, that she may not spare
the traitors, and that her safety is precious to God.

O mightier daughter of a mighty father and fairer daughter
of a mother fair! O Queen, next to the gods the strength
and summit of our estate!

Say, divine virgin, what was your thought, what colour
showed itself in your bright cheeks, when lately the
first news of traitors shocked your ears?

Ecquid timebas? ecquid et in genis
Pallor sedebat? pectoris O fides:
Non tu timebas virgo multos,
Cerulea canes, placida agna tygres.

Illud gemebas, quod fuerat tibi
Stringendus ensis; quid doleas tamen?
Effer secures, et nefandum
Poena comes scelus insequatur.

Tichburne (quaeso des veniam Anglia,
Et diua virgo) me miseret tui;
Dignaeque fato molliori
Salsberii miseret iuuentae.

Non illa mens est, non animus mihi
Mordere Manes; non ego mortuis
Insulto laetus, non cruoris
Ulla mihi subijt voluptas.

Odi cruentum supplicij genus;
Vester redundet sanguis ei in caput,
Qui crimen ingens suasit, at nos
Nulla grauet sobolemue culpa.

Sed charitates continet omnium
In se una cunctas patria nobilis.
Tichburne, iam nec me tui, nec
Salsberij miseret iuuentae.

Tu me seuerum patria, tu facis
Regina, durum: me capitis tui
Regina chari, me tuorum,
Me patriae miseret, meique.

Semperne strictas ut latus in tuum
Sicas timeres? tuta foris, pedem
Nunquamne figas? tune auito
Ut solio trepides inulta?

Nos, Proditoris ludibrium improbi
Et praeda, simus? nos miseros neci
Designet impune, et superbum
Instituatur, duce te, triumphum?

Illi periclo dispereant suo
Nati gygantum sanguine; spiritus
Contunde sublimes, malumque
Eueniat male cogitanti.

Pindo Tiphoeus Pelion obruat,
Ossamque Olympi mole cacuminet,
Frendant Gygantes, et reuulsas
Enceladus iaculetur ornos:

Maiores, trisulco fulmine, Iuppiter
Sternet rebelles, impiger aggeres
Etert, aeternumque flammis
Sulphureae cruciabit Aetnae.

Did you fear aught? did any paleness show in your cheeks?
O confidence of heart! You, a virgin, feared not the many
men; a doe, feared not the dogs; a quiet lamb, the tigers.

At this you grieved: that you had to draw the sword.
Yet why lament? Bring out the axes, and let meet
punishment follow upon the accursed crime.

Tichborne, I pity you,—pray grant me pardon, England,
and royal Virgin! And I pity the youth of Salisbury,
worthy of a gentler fate.

That is not my spirit; it is not my disposition to gnaw
at ghosts, I do not gladly triumph over the dead, nor have
I ever felt any pleasure in blood.

I hate the gory type of punishment; let your blood flow
upon the head of him who instigated this enormous crime,
but let no guilt oppress us or your progeny.

Yet our one noble fatherland embraces in itself every
devotion of us all. [In view of that,] Tichborne, I now
pity neither you nor Salisbury's youth.

Fatherland, you make me harsh; Queen, you make me
hard. What I pity, O Queen, is your dear head and
your subjects, my country and myself.

Are you always to fear daggers unsheathed against your
breast? Are you never to set foot abroad in safety?
are you to tremble on your ancestral throne and have
no redress?

Are we to be the jest and prey of a wicked traitor? Is
he with impunity to mark us wretched ones out for slaughter
and organize a proud triumph while you are Queen?

By their own peril let these sons of the giants' blood be
undone; crush their arrogant spirits: Honi soit qui mal
y pense!

Let Typhæus overwhelm Pelion with Pindus and set
Ossa as a peak on the mass of Olympus; let the giants
rage, and Enceladus hurl uprooted wild-ash trees:

Let Jupiter with his greater power lay low the rebels
by three-forked lightning, let him strenuously overthrow
their preparations, and torment them forever in the flames
of sulphurous Aetna.

Titana proles consilij fere
 Expers, ruinam mole trahit sua.
 Odere Diui quicquid altum
 Tentat iter, vetitumque nobis.

Caelo minatur qui solio inuidet:
 Cognata regum est conditio Ioui:
 Quos qui lacessit fraude, seu vi,
 Ille Deum petit impotenter.

Unquamne surgat tam nigra lux mihi
 Qua caesam Elisam vulnere defleam?
 Non illa lux surget, Deusue
 Tale nefas patietur unquam.

Nec te venenum, nec dolus auferet,
 Nec sica, nec vis; molliter occides
 Matura fatis, haec Sibyllam
 Crede tibi cecinisse vatem.

Serenissimae Reginae nostrae Elizabethae, tot
 capitales perditorum hominum insidias, im-
 meritissime indignissimeque factas esse,

ODE 7

Miretur aetas postera sanior,
 Cur Proditores nostra tot extulit:
 At cur Elisae tot pararunt
 Exitium, merito stupescat.

This offspring of Titans, almost devoid of reason, invites
 ruin by its very size. The gods hate whatever attempts
 a too arrogant course and one forbidden to us.

He who is hostile to the throne is an assailant of heaven;
 the state of kings is allied to God; he who injures kings
 by fraud or force is ineffectually attacking God.

Can so black a day ever dawn for me whereon I am to
 mourn Eliza violently slain? No such day will dawn,
 nor will God ever suffer such an iniquity.

[O Elizabeth,] neither poison, nor trickery, nor dagger,
 nor force shall take you off. Gently you will die, ripened
 by the fates. Have faith that the prophetess Sibylla has
 made you this prediction.

ODE 7

That all these mortal plots of abandoned men against
 our most serene Queen Elizabeth have been made
 most undeservedly and unworthily.

A later, saner age will wonder why ours brought forth so
 many traitors. Yes, it may justly be astounded why so
 many attempted Eliza's death.

Non Frater istas iam puer, aut Soror
 Sensere fraudes, non Pater inclytus
 Henricus armis, non, amicus
 Pacis, Auus, proauique Reges.

Num Frater illam mente pia, Soror
 Clemente vicit? num Pater ardua?
 Prudentiae num laude neptim
 Vicit Auus, proauique Reges?

Quando illa tantum commeruit nefas?
 Qua parte peccat? quo scelere est nocens?
 Tantas quid iras concitauit
 Non nisi caede fera expiandas?

Quando illa dulcem saeua virum abstulit:
 Quando reliquit? num tragico dedit
 Dignas theatro nuptiales
 Tot populi Procerumque strages?

Quem laesit unquam? quos nisi perdit
 Ferro irruentes sponte sua, piger
 Percussit ensis? queis libido est
 Carnifices hebetare cultros.

Si quaerat illa; en, cuius ego bouem
 Aut cuius agrum detinui, malum
 Cui fraude feci? an non Britanni
 Id referant? Nihil abstulisti.

No such treasons did her brother experience, though but
 a boy; nor her sister; nor her war-famed father Henry;
 nor her grandfather, that friend of peace, and the preceding
 kings.

Did her brother surpass her in piety, or her sister in
 mercy, or her father in vigour? In fame of prudence
 was this scion inferior to her grandsire and the preceding
 kings?

When has she merited such outrage? In what point does
 she sin? of what crime is she guilty? What has engendered
 such hostilities, expiable only by savage slaughter?

When did she cruelly slay a tender husband? when did she
 abandon one? Has she been guilty of nuptials worthy of
 the tragic theatre and innumerable murders of populace
 and nobles?

Whom has she ever injured? Whom has her unwilling
 sword smitten, except those that of their own will rushed
 desperately upon her with their weapons, those who have
 a lust for blunting the knives of the executioner?

If she ask, 'Lo, whose ox have I taken, or whose field?
 whom have I defrauded?' may not the Britons answer thus,
 'Thou hast not taken aught?'

Non illa Circe est, non animi impotens
 Medea, ferro, perfide, quam petis?
 Cur stringis ensem? siste, Elisa est,
 Cui properas aperire pectus,

Quacunq̃ curru sol habitabiles
 Illustrat oras, optima principum:
 Regina virgo, cui quid aetas
 Nostra videt simile, aut videbit?

Percurre Reges, quos habet undique
 Immensus orbis (liuor edax meis
 Absit Camaenis) inter omnes
 Luna micat, velut inter astra.

Cuius beaut tot meritis Deus
 Tam mite regnum, dum misere fremunt
 Armis, et ardent Marte gentes,
 Alta suos tegit umbra pacis.

Priuata sceptro si posito foret,
 Quis non Elisam diligeret tamen?
 Cui non placeret? quis potenti
 Imperio genitam negaret?

Quae forma vincens Sithoniam niuem?
 Quae vita? quae mens? quae sine crimine
 Dulcedo morum? absolueretur,
 Inuidia licet assidente.

She is no Circe, no brainsick Medea. O traitor, whom
 are you threatening with your blade? why do you draw
 your sword? Stop. It is Eliza whose heart you strive
 to pierce,

The best of princes through all the lands that the sun
 lights with his chariot and makes habitable; a virgin
 queen, whose like our age sees not, and shall not see!

Consider the kings whom our boundless world possesses
 in all its parts. Far be carping belittlement from my
 verses, but she shines among them all like the moon amid
 the stars.

God has blessed her gentle reign with countless benefits.
 While the nations [abroad] groan miserably under arms
 and blaze with war, the deep shadow of peace enfolds
 her subjects.

If she should lay aside her sceptre and live as a private
 person, who would not nevertheless love Eliza? who
 would not admire her? who would deny that she was born
 for sovereign power?

What beauty, surpassing Thracian snow! How good a life,
 and what a mind! what blameless sweetness of disposition!
 She would be exonerated even though envy were her judge.

Laus ergo sane est magna, viri cadat
 Si virgo dextra, si rapiat piam
 Miluus columbam, vultur agnam,
 Sanguineo lupus ore ceruam.

Gaudetne caesa virgine Caelites?
 Haec placat illos victima? cur Deos
 Praetendis insontes? Elisam
 Cur gladio petis innocentem?

Crudele pectus, Proditor, exue:
 Vagina ferrum condant, et excute
 Sensus nefandos, et cruore
 Parce pio scelerare dextram.

Ad Christianos Reges, ut transfugas
 Proditores finibus suis exterminet.

ODE 8

Saluete Reges, progenies Deūm
 Et certa proles, imperium quibus
 Caelo secundum, vestra virtus
 Et Superi faciles dederunt:

Seruante cauti sceptrā, satellites
 Fidi coronent; Proditio furit:
 En sanguinis vestri nefanda
 Quae subijt sitis hauriendi?

A noble exploit, then, it surely is, if the virgin fall by
 some man's hand, if the kite seize upon the gentle dove,
 the vulture on the lamb, the wolf with gory mouth upon
 the doe!

Do the immortals delight in a virgin's murder? does such
 a victim propitiate them? Why do you invoke the un-
 sinning gods? why do you attack innocent Eliza with
 your sword?

Rid yourself, Traitor, of your cruel heart; let the sheath
 hold the dagger; renounce your execrable purposes, and
 desist from polluting your hand with righteous blood.

ODE 8

To the Christian kings, that they may exterminate
 the escaped traitors in their territories.

Hail, ye Kings, offspring and undoubted issue of the gods,
 to whom your own merit and the gracious immortals
 have given a power next to heaven:

Protect your sceptres carefully, and may faithful guards
 encompass you! Treason is raging. Behold, what an
 accursed thirst has grown to shed your blood!

Vos, Proditores hospitio procul
Arcete regni. perniciem trahent
Exempla vestris, totum ouile
Tabida ouis vitiabit una.

Ad nostrates Anglos, ut quibuscunque partium
studijs ducti, externum dominatum
omnes abominentur,

ODE 9

Quae grande mens est ausa nefas semel,
Claroque gaudens sanguine dextera
Nunquam quiescet, nec colorem
Lana bibit vitiata primum.

O Luce dulci Patria dulcior,
Et chara Tellus, pars animae meae
Non parua, ductricem Britannam
Compositis odijs sequamur.

Impune per vos in dominans caput
Audebit oris Proditor improbi?
Impune maiestas iacebit
Quisquilijs hominum terenda?

Quaecunque nostras religio imbuit
Mentes, Elisam praeferat extero.
Quaecunque discordes fatigat,
In patriam pia nulla suadet.

Unita sors est tot dominantium;
Quenquam quod urit, quemque premat
malum.
Ardente vicini camino,
Vestra domus caueat fauillas.

Quam solus ut tu mente regas tua
Vis esse nullam, Proditor? extera
Suspecta vis est, nec recedet
Turba valens, sitiensque regni.

Quo Musa tendis? desine Regibus
Garrire. nostram summa brevis decet
Legationem, longiore
Purpureas onerabis aures.

Ut sana fiat Patria, sauciam
Hostine trades, qui solidas simul
Partes aduret, qui secabit?
Horribilis medicina bellum est.

Hear ye! Keep traitors far from the shelter of your
kingdom. Their examples will carry the bane to your
people; a single diseased sheep will corrupt the entire flock.

The mind that once has attempted a colossal crime, and
the hand that craves the blood of rulers, will never rest;
wool that has been stained will not take its original
colour.

Shall the evil-faced traitor make his attempt upon a
crowned head uncontrolled by you? shall majesty lie at
the mercy of the dregs of mankind, with no redress?

The destiny of the many rulers is a joint destiny; the
danger that afflicts any one may threaten every one.
When your neighbour's chimney is afire, let your own
house beware of sparks.

Whither are you ranging, Muse? Cease to prate to the
kings. A brief compass fits our message; with a longer
one you will weary their noble ears.

ODE 9

To our English fellow-countrymen, that, with whatever
zeal of party they are moved, they may all
abhor the rule of foreigners.

O country sweeter than the sweet light of day, dear
native land, a great part of my soul! Let us make up
our quarrels and obey our English governess.

Whatever religion colours our minds, let it set Eliza
above an alien. Whatever religion vexes us with discord,
no righteous one impels us against our country.

Do you alone, Traitor, wish it annihilated, that you
may rule according to your will? Foreign power is to
be mistrusted, and a strong force, thirsting for sovereignty,
will not withdraw.

To make our country well, will you deliver it wounded
to the enemy, who will burn and slash its intact parts?
War is a horrible medicine.

Quo prisca virtus, quo recidit vigor
 Innatus Anglis, indocilis pati
 Nutus heriles transmarini
 Imperij, regimenque durum?

Hos miles agros, has segetes metet
 Hispanus, auro, non numero valens?
 Haec arua Gallo conseruntur?
 Haec mea sunt, veteres coloni

Migrate, victor dicet? et insolens
 Caedet morantes? nos taciti metu
 Ceruice submissa, superbi
 Turpe iugum domini feremus?

AEterna me nox ante, precor, tegat,
 Ensisque tollat vulnere patrius;
 Seruire fas O sit Britanno;
 Seruitium domino leuatur.

Whither has departed from the English their former
 valour and the inborn robustness, incapable of suffering
 the lordly commands and hard yoke of an empire across
 the sea?

Shall the Spanish soldier, strong with gold, not men,
 reap these meadows and cornfields? Are these lands tilled
 for the Frenchman? 'These are mine,' shall the victor say?

'Move out, ye ancient occupants!' And shall he wantonly
 kill those who delay? Shall we, speechless with fear,
 bear with hanging heads the base yoke of an arrogant
 master?

Sooner, I pray, may eternal night enclose me, and my
 father's sword wound me to death! Be it my lot to serve
 a Briton! Servitude is alleviated by the [quality of the]
 master.

THE SHIP OF THE SOUL ON A GROUP OF GRAVE-STELAE FROM TERENCE

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(Read April 26, 1941)

ABSTRACT

In this paper four small grave-stelae from Terenuthis in lower Egypt are illustrated, and their interpretation is discussed. The period of the burials was at the end of the fourth or the beginning of the fifth century of the Christian era. In all four examples a figure representing the deceased person is in a boat or is about to enter one. It is well known that the ancient Greeks often compared human life to a voyage, and the imagery connected with the ship of life was taken over by the Christians. In consequence of this, the ship-symbol occurs on a number of Christian tombs in the catacombs of Rome. In previously published material from Christian Egypt, this symbol is rarely found; and yet the Christian idea of the ship of the soul divinely guided to its final harbor was probably accepted all the more readily in Egypt, because the people had inherited from dynastic times the belief that the soul was carried in a boat to the abode of the blessed, sometimes with the guidance of a divine ferryman.

In the spring of 1935 an expedition of the University of Michigan under the direction of E. E. Peterson excavated a cemetery of the late fourth and early fifth centuries of our era at Kom Abu Billu in lower Egypt. This place is thought to be the site of the ancient Terenuthis or the necropolis belonging to that town. It is just west of the western or Rosetta branch of the Nile, about ten miles from Kafr Dāfūd, and on the road to the Wadi Natrun. Among the objects discovered were a large number of limestone grave-stelae of moderate or quite small sizes; an area of 18 × 18 inches would accommodate almost any one of them, and many are much smaller. These stones were set into the grave-mounds themselves; Fig. 1 shows in its original position one of the stelae that will be examined in detail later. It is set in a sort of recess in one end of the built-up mound, as if it closed an entrance to the grave. The structure of some of these mounds is quite peculiar, but the description of them belongs to the report of the expedition and cannot be undertaken here.

The workmanship of these sculptures is poor. On several of the stelae, including the group to be discussed in this paper, the designs are outlined by the simple method of incision below the level

of the original plane of the slab, and the background is not cut away. As a result, the shadows are deep, and detract not a little from the effect of the designs. Considerable traces of color remain on many of the specimens.

About 125 of these grave-stelae are now in the Museum of Classical Archaeology at the University of Michigan. Many of them show with somewhat monotonous regularity a design representing the deceased person reclining upon a couch at a banquet; he usually holds a cup in his extended right hand, and a table with various articles of food and certain other objects stand



FIG. 1.



FIG. 2.

beside the couch¹ (Fig. 2: 29.7 cm. high, 20.7 cm. wide). We shall have occasion to return to this design later for a special purpose.

There are four stelae that present a different design, in which the figure of the deceased is either in a boat or is about to enter one. This group attracted my attention because I had

¹ Pictorial representations of the banquet in heaven are discussed by C. M. Kaufmann, *Die sepulcralen Jenseitsdenkmäler* (pp. 194-206, *Die Darstellungen des himmlischen Gastmahles*). The idea of feasting in the other world is of course very ancient, and doubtless grows out of a belief that the wants of the dead are like those of the living; Greek grave-reliefs of heroes feasting are well known. Leaders of the Orphic sect were said to promise their followers a banquet, and even eternal drunkenness, in the other world. The authorities are listed in Rohde, *Psyche*,¹ I, p. 315, n. 2, II, p. 129, n. 3; see also Guthrie, *Orpheus and Greek Religion*, pp. 158-160. For the "Hero-Feast" and its possible relation to the Orphic doctrine (with some cuts of typical reliefs), see Harrison, *Prolegomena to the Study of Greek Religion*,² pp. 349 ff., 614. There is little doubt that Greek reliefs depicting this subject exerted the principal formative influence upon the pattern of the Terenuthis stelae that represent the dead at a banquet.

recently been interested in the symbolism of the ship or boat; and I am publishing these four by the kind permission of the authorities of the Museum.

The inscription upon the first of these stelae (Fig. 3: 25 × 21 cm.) shows that it is the monument of a young man named Apion, twenty-six years old.² He is standing with both hands raised as if in prayer, an attitude known from many Christian monuments not only in Egypt but also in Rome.³ He is in a small boat with steering-paddle, but no sail. Its shape is much like that of the boats so well known from the sculptures and paintings of dynastic Egypt. The work, which is very crude, continues a tradition of much earlier reliefs and paintings in representing the lower part of the body and the feet in profile although the figure faces front.



FIG. 3.

² The second numeral, the so-called stigma, is so low and flat that the reading might be doubted; but the sign occurs in just such a form on many documentary papyri of the period.

³ Examples from Roman monuments may be seen in Garrucci, *Storia dell' arte cristiana*, tav. 482, 485. Boldetti, *Osservazioni sopra i Cimiteri*, pp. 369, 372, 377, 378; for Egyptian examples, see Crum, *Coptic Monuments*, Pl. XLIX-LIII (Catal. gén. des antiquités égyptiennes du Musée du Caire, 1912).

The second is even cruder (Fig. 4: 28 × 22.5 cm.). Here the deceased is in a squatting position in the boat. There is no inscription; the angular cuts at the bottom are not letters but a suggestion of the ripples of the water. There are traces of red paint on the head, neck and arms of the man.

Next in order is a specimen that is something of an archaeological curiosity (Fig. 5: 14 × 20 cm.). Here the dead man is represented as reclining in a boat, which has a mast, yard and sail. His right arm is extended towards and a little beyond the mast, but is not, as might be thought at a careless glance, engaged with any



FIG. 4.



FIG. 5.

part of the tackle. As a matter of fact, the right hand holds a cup, as if he were at dinner; and thus it is apparent that the stone-cutter has simply combined two designs, and that very awkwardly. Taking the reclining figure from the often used pattern of the banquet, he has simply imposed it upon the boat; and in doing so he has placed the man with his feet to the paddle, in a position where he could not use it, even if one hand were not occupied with the incongruous

cup, and he has neglected to bring the mast into connection with the hull of the boat.

The fourth of these boat monuments has two parts in its design (Fig. 6: 50 X 23 cm.). In the left background, on the shore of a stream, stands a female figure with the hands raised in the posture of prayer. Her chiton, or undergarment, is a dark sea-green; all other colors are destroyed. Out in the stream is a boat similar in design to that seen in Fig. 3; in it sits a youthful male figure. Here also the design of the banqueter has had some influence; for the left elbow and part of the forearm of the man in the boat rest upon a cushion, as in the banquet-monuments, and the hand in consequence is held straight out instead of resting upon the steering-paddle. But the sculptor has given the right hand something to do. It seems to be drawing upon a rope attached to the yard as if to swing it around to a new position, probably, as we shall see later, in order to lay the boat alongside the shore. The water is indicated, as in a previous example, (Fig. 4) by an angular ripple.

Before dealing with the interpretation of this monument it is necessary to rehearse briefly what is known of the symbolism of the boat in Christian times, and that cannot be done without some reference to the occurrence of that symbolism in pagan literature. There is no need to go into details, for the topic has been treated, more or less fully, by several writers.⁴ First, then, there is abundant literary evidence that from an early period the seafaring Greeks saw a certain analogy between the vicissitudes of human life and the dangers and hardships of a sea-voyage. Here we are concerned not so much with passages like Alcaeus' famous metaphor in which the strife-torn state is compared to a ship in a storm,



FIG. 6.

⁴ As far as I know, nobody has attempted to gather all similes or metaphors in which a ship plays a part. J. Kahlmeyer, in his Greifswald dissertation, *Seesturm und Schiffsbruch als Bild im antiken Schrifttum* (Hildesheim, 1934), does not limit himself to figures involving storm and shipwreck, but touches also upon other images of nautical origin. In pp. 272-286 of F. J. Dölger's *Sol Salutis* a number of important literary and archaeological treatments of the symbolic ship are cited; the author is particularly interested in the eastward direction of the ship in connection with the eastward position in Christian worship. W. Vollgraff, discussing the Delphic paean, has collected many examples of metaphors based upon the idea of a harbor (*Bull. de corr. hellén.*, XLVIII, pp. 178-186); and the present writer, in *Harvard Theol. Rev.*, XXXIV, pp. 49-67, has dealt more fully with the same subject and related ideas. This last paper will be referred to later by its title, "Desired Haven," and its pages.

as with utterances like Plato's phrase "this voyage of life," where he has in mind the individual rather than the community. The idea that a god might guide an actual ship and deliver the mariners from danger is found in Homer and Aeschylus, and philosophers talked of divine guidance in the voyage of life, although to some of them it seemed that it was merely the goddess of chance who steered the vessel of human fortunes. The last voyage of all ended in the harbor of death; and in a solemn passage of his *Seven Against Thebes* Aeschylus sings of the dark ship that passes over Acheron bearing its freight of souls to the sunless land. It will be remembered that according to a popular belief, the soul had a companion on this voyage across the dark water. This was the gloomy and morose Charon, a daemon of death, who ferried the soul across to its abiding-place.⁵

Thus far, then, we see that a boat guided by a daemonic ferryman played a part in a genuine popular belief of the Greeks, and that quite apart from that bit of folk-myth, both poets and philosophers often thought of life as a voyage, in which a divinity might be at the helm of the ship. In falling heir to pagan thought, Christianity naturally rejected the myth of the hateful Charon; but the figure of the voyage of life, or the ship of the soul, was not only unobjectionable in itself, but it could also be used for edification in connection with incidents of both Jewish and Christian sacred narratives. Some of the Church Fathers used the ark of Noah as a type of the Christian congregation, made up of men and women of all conditions; to others the story of Christ stilling the tempest on the Lake of Galilee suggested the image of the Church as a ship struggling with the storms of the world, with Christ as pilot, the apostles as officers, and all the members of the Christian body as crew or passengers. But along with the image of the ship as the church, there persisted the idea of the ship as the type of the individual life, guided by Christ as pilot and master, and that figure enters into a number of hymns and hortatory writings. It is not surprising that Clement of Alexandria mentions a ship sailing before a favorable wind

among the devices that are appropriate for a Christian's seal-ring.⁶

This literary and theological tradition would seem to be enough to account for the use of the symbol of the ship in connection with Christian tombs anywhere. The archaeological material illustrating this symbolism, so far as it comes from Roman tombs and catacombs, has been collected and ably examined, especially by Catholic scholars.⁷ A few examples of it may be cited as analogues to the Terenuthis stelæ. There is an inscribed slab from the cemetery of Prætextatus on the Appian Way, bearing the name of Aelia Eusebia, and below it a ship sailing to the right—that is, to the sunrise—with a figure in the bow, unfortunately indistinct.⁸ Much better known is a famous bronze lamp in the form of a ship, now in the Uffizi in Florence.⁹ In the bow stands a man in the attitude of prayer, while another sits holding the steering-paddle at the stern. To the mast is fastened a tablet with the inscription *Dominus legem dat Valerio Severo Eutropi vivas*. As the inscription suggests, and as the object is generally interpreted, the figure at the helm is Christ, and the man in the bow is Valerius Severus Eutropius, to whom the lamp may have been presented. Of other examples, perhaps the most interesting is a slab showing a ship approaching a harbor, which is indicated by the lighthouse just ahead of it.¹⁰

Since our stelæ are from an Egyptian site, it is natural to inquire whether there were specifically Egyptian ideas or customs that rein-

⁵ A number of passages showing the symbolic use that Christian writers made of the ship, the harbor, and ideas connected with them are cited in "Desired Haven," pp. 59-64. For the ark as the type of the Church, Hippolytus, *Elench.*, 9. 12. 23 is important; for elaborate comparisons of the Church, with its institutions and its hierarchy, to the parts and the crew of a ship, see Hippolytus, *de Antichristo*, 59, and [Clem.], *Epist. ad Jacob.*, 14 (Patrologia Graeca, II, 49). Clement's words about the ship as a seal-device are to be found in his *Paedagogus*, 3. 59. 2.

⁷ De Rossi, in Pitra, *Spicil. Solesm.*, III, p. 563; Wilpert, article "Schiff" in F. X. Kraus, *Realencyklop. der christl. Altertümer*; Kaufmann, *Jenseitsdenkmäler*, pp. 178-186.

⁸ Published by Kanzler, *Nuovo bulletino di arch. crist.*, XV, p. 124, Fig. 8.

⁹ Garrucci, *Storia dell' arte cristiana*, VI, tav. 469, 1; on a smaller scale, but more accurately reproduced in Kaufmann, *Handbuch der christl. Archäol.*,² p. 296, Abb. 147. Wilpert, *Die röm. Mosaiken*,² I, p. 303, thinks the helmsman must be Paul, rather than Christ, because of his baldness.


¹⁰ Garrucci, *op. cit.*, tav. 486, 20.

⁵ The passages to which this paragraph refers are as follows: Alcaeus, fr. 30 (Diehl); Plato, *Laws*, 803 b; Homer, *Odys.*, 9. 142-143; Aesch., *Agam.*, 661-666; *Seven*, 854-860. A number of allusions to the haven of death will be found in "Desired Haven," pp. 51-53; and on pp. 57-59 the philosophical use of the figure is illustrated.

forced the general Christian tendency to employ a ship as the symbol of a soul, and the answer is definitely affirmative. Many Egyptian towns had their cemeteries on the other side of the Nile, and the last journey of many a man was made in a boat. Further there is both monumental and textual evidence from various periods that the soul of the deceased was believed to be carried in a boat to the region of the blessed.¹¹ In particular certain chapters of the *Book of the Dead* mention the ferryman of Osiris, who conveys the soul that is "true of word" to the abode of the god. There are also special charms to secure for the soul the use of a boat for his voyage; so, for example, the ninety-ninth chapter of the Theban recension, "Of bringing a boat in the Other World," which has for its vignette in several papyri a picture of a boat with the dead person sitting or standing in it.¹² As for the divine companion, the soul is sometimes pictured in a boat with Ra and other deities. The divinity in a boat continued to be a familiar concept long after the dynastic age. In the Roman period we hear much of the great festival of the Ploia-phesia or *navigium Isidis*, in which the ship of Isis was launched; and many coins show the goddess standing upon her ship, holding a corner of the swelling sail.¹³ As a final bit of evidence from Roman times I may mention the scores of amulet-stones with a representation of the infant Horus, or Harpocrates, seated upon a lotus in a papyrus boat.¹⁴

No country has ever been more tenacious of ancient beliefs and ancient ways than Egypt. The custom of mummifying the dead lasted for some time after the introduction of Christianity. Sacred animals of the old religion, such as the hawk, the cat, and the jackal, are sculptured upon some of the Terenuthis monuments; and at a period much later than that of the necropolis of Terenuthis the cross on Coptic grave-stones sometimes has the form of the ancient *ankh*, the

hieroglyph of life. Hence there is much reason to think that the Greek-Christian idea of the voyage of the soul, with the ship as its symbol, was readily accepted by the Christians of Egypt, not as something entirely new, but as a new application of an ancient idea. Yet actual examples of the soul-ship seem to be rare in Christian Egypt, unless they are hidden among unpublished material, and that rarity may lend a special value to these rude grave-stones from Terenuthis.

We are now ready to consider the interpretation of the fourth of these boat-monuments (Fig. 6). Since there is no inscription, and since no other remains have been preserved to indicate whether the entombed body was that of a man or a woman, one might perhaps conjecture that the figure in the boat represents the soul of a dead man setting out on his voyage to the land of spirits, and that the woman on the shore is a mourner. But this seems to be contradicted by the fact that on very many of these monuments it is certainly the deceased who is represented with his hands raised in prayer. In the opinion of de Rossi and Kaufmann, the praying figures on Roman tombs regularly represent souls in a state of blessedness. The Egyptologist Ebers even conjectured that the frequent occurrence of these *orantes* on Coptic grave-monuments was partly to be explained by the influence of the old hieroglyph for the *Ka*, the double or personality-soul, which was indicated by a pair of arms raised in the position ¹⁵

It seems more likely, then, that the figure on the shore is that of the dead woman to whose tomb this stela belongs. Who, then, is the boatman? Certainly not the Charon of Greek popular belief, for he is regularly represented as a grim, uncouth elderly man. Nor is it likely to be John the Baptist, who, according to a curious Coptic sermon, received a strange commission from Christ: if any man had while living celebrated the commemoration of the Precursor, John should transport his soul in a golden boat across the river of fire in Amente.¹⁶ Rather, we must turn for the explanation to the Church Fathers, who so often speak of Christ as the kindly pilot of the soul in life and death; thus we find the closest analogue to this monument in the

¹¹ Erman, *Die Religion der Aegypter* (1913), p. 217; Budge, *The Mummy*, pp. 463-466.

¹² Good illustrations in L. Speleers, *Le Papyrus de Nefer Renpet*, Pl. XX; E. Naville, *The Funeral Papyrus of Louisa*, Pl. XXIII.

¹³ Good illustrations may be seen in Alföldi's *A Festival of Isis in Rome* (Dissertationes Pannonicae, Ser. II, fasc. 7, 1937), Pl. I, 1, 2, 7; IV, 1, 2, 6; XVIII, *passim*.

¹⁴ Since stones with this design are usually classed with the despised "gnostic" gems, the available illustrations are few as compared to the large number of existing specimens; see, however, *Catalogue of the Southesk Collection*, I, Pl. XV, n. 54; Budge, *The Mummy*, p. 330 and Pl. XXIV; *Journ. Egypt. Arch.*, XVI, pp. 6-9.

¹⁵ Kaufmann, *Jenseitsdenkmäler*, p. 109; *Handb. der Christl. Arch.*,³ p. 272, and n. 1; Budge, *The Mummy*, p. 340, n. 1.

¹⁶ Budge, *Coptic Apocrypha in the Dialect of Upper Egypt*, p. 347.

bronze lamp in Florence that was mentioned a short time ago. The makers of these objects would have understood and appreciated the imagery of Tennyson's "Crossing the Bar".

Since the boat-symbol seems to be rare in Egypt of the later age, it may be worth while to mention the only other examples of it that have come to my attention. One, published by Dr. W. E. Crum in his *Coptic Monuments*, is the grave-stone of a monk named Peter (Fig. 7).¹⁷



FIG. 7.

Above are three crosses, right and left a *crux ansata*, in the middle a *crux monogrammatica* (derived from a combination of the letters X and P, for Christ). Below, a ship, not occupied by a human figure. Amidships a device that was probably meant for the monogram $\chi\rho$, although the loop of the P is merely suggested by the line dividing the two panels, and one of the diagonals. It may have been originally shown by the use of paint. Besides this grave-stone, we find a ship used as one of the types of decoration for the pilgrims' bottles known as Menas flasks or ampullae, because they were manufactured in great numbers to contain the holy water and holy oil dispensed at the shrine of St. Menas in the Mareotic desert.¹⁸ But as used on these flasks the ship has no funerary suggestion; it is merely a symbol of the Christian life, like the seal-rings that Clement of Alexandria approved.

This discussion of the soul-ship may be closed with the pathetic words inscribed upon the tomb

of a certain Cosmas.¹⁹ The composer of the Coptic epitaph makes the dead youth say:

O journey to a strange land, farther than ever before! O voyage in which it is hard to come to the other shore! The sea is wide, its waves are wild, and little is my boat—the youth of my body, the brief count of my years.

POSTSCRIPT

After the foregoing paper had been sent to the editors some further material bearing upon the symbolism of the ship was brought to my attention, and I append it here. My colleague Professor Richard Ettinghausen referred me to Beyer and Lietzmann's *Die jüdische Katakomben der Villa Torlonia* (1930), Pl. 18d, an illustration of a ship that was scratched into the plaster of a *loculus*. The ship has a sail and two steering-paddles, but no person is seen on board, and there is no inscription. It would seem to be the symbol of the life-voyage or of the departed soul, but there is no definite proof of this. The reference to the soul-ship seems to me to be clearer in a monument to which Professor David M. Robinson called my attention. This is the funerary stela of Kallineikos, which was first mentioned by Professor Robinson (*Am. Jour. Philol.*, 27, 1906, 448), and was subsequently published by A. Salač (*Bull. de corr. hellén.*, 44, 1920, 354-357). At the top are two busts, one of a bearded man, the other of a boy. The main inscription has to do with the death of the older man, Kallineikos; but it also mentions his younger brother, who seems to have died some time before. At the bottom of the monument is a large ship followed by a quite small one; the rigging shows that this smaller vessel is a true ship, not a dinghy attached to the larger one. It seems fairly clear that the two ships of different sizes represent the souls of the two men of different ages, and do not, as Salač thought, refer merely to the fact that Kallineikos was a ship-master (*ναύκληρος*).

I am further indebted to Professor Ettinghausen for a reference to two peculiar mummy-paintings that were shown by the Brooklyn Museum in its exhibition held early in 1941, and

¹⁷ No. 8574, Pl. XXX.

¹⁸ See Kaufmann, *Die Menasstadt*, I, Pl. 96, 10, 11, 12.

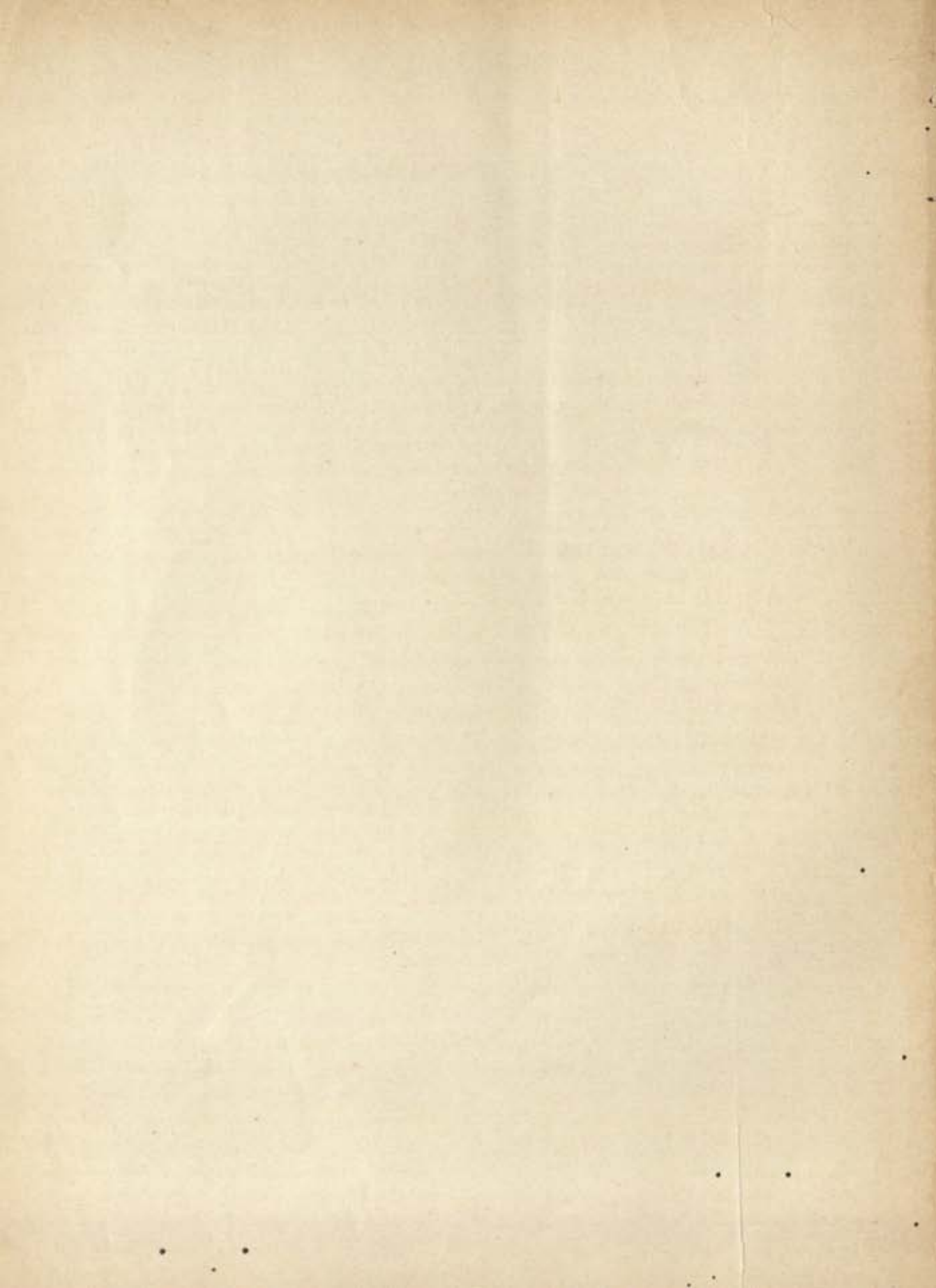
¹⁹ Crum, *Coptic Monuments*, no. 8706, Pl. LV; Mallon, *Coptica* (Mélanges de la faculté orientale, Université Saint Joseph, V, 2), p. 125.* The date of the monument is 786 A.D.

subsequently published in the volume *Pagan and Christian Egypt*, Nos. 9 and 10; one of these belongs to the Boston Museum of Fine Arts, the other to the Brummer Gallery. The designs are almost identical—a portrait of the deceased above, holding a cup in one hand and in the other an object that is doubtfully described in the Boston painting as a sheaf of wheat, in the other as a garland. I incline to think that in both examples it is an ear, or bunch of ears, of wheat. Below is the "Sokaris bark flanked by jackals". Sokaris (Sokar, Seker) was a Memphite god of the dead who was more or less identified with, or even superseded by Ptah and Osiris (Erman, *Die Religion der Aegypter*, 26); the boat is well illustrated and discussed in Budge, *The Gods of the Egyptians*, I, 504–506. Thus these two paintings seem to carry on the tradition of the soul-

ship which we find in the vignettes of the Book of the Dead.

Attention was called in the article mentioned above (*Harv. Theol. Rev.*, 34, 60–62) to the frequent occurrence of figures of speech based upon the ship or the haven in Manichaean psalms. A passage which might well have been cited there shows that the idea of Jesus in a boat was a fixed element in the Manichaean mythology; this is to be found in Epiphanius *Haer.*, 66, 31 (III, 71 in Holl's edition) in a list of the "emanations": αἱ δὲ προβολαὶ πᾶσαι, ὁ Ἰησοῦς ὁ ἐν τῷ μικρῷ πλοίῳ, καὶ ἡ μήτηρ τῆς ζωῆς, καὶ οἱ δώδεκα κυβερνήται, καὶ ἡ παρθένος τοῦ φωτός, κτλ. See also a short paper by S. Eitrem, "De servatore mundi navis gubernatore" in *Collectanea Neotestamentica* (ed. A. Fridrichsen, Uppsala, 1940), IV, 5–8.

C. B.



LONG ENDURING METEOR TRAINS

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(Read April 24, 1941)

THIS research is a continuation, along additional lines, of that by the late C. C. Trowbridge, which appeared during the years 1907-1911. It was made possible by a grant of \$1000 from the Penrose Fund of the American Philosophical Society in 1935. With this Dr. C. H. Clemminshaw was brought to the Flower Observatory and for about eight months devoted his day work to meteor train phenomena. On his resignation, I took the work over completely and, as my other duties permitted, have slowly pushed it to a conclusion. During the past several months I have been efficiently aided by my wife, Mrs. N. S. Olivier, who has examined hundreds of volumes for references and aided in preparing the data. To both her and to Dr. Clemminshaw I am under deep obligations.

The data here presented came from the following sources. (1) All the records gathered by Trowbridge and turned over to me by the Meteor Committee of the National Academy of Sciences. (2) The records collected by our own member, the late Prof. Cleveland Abbe, Sr. (3) The immense mass of data in my hands, due to the work of the American Meteor Society. (4) Records sent to me privately by astronomers, mostly foreign, in greatest number from the U.S.S.R. (5) Reprints on all phases of meteor work sent me from many countries. (6) Examination of from 2000 to 3000 scientific journals and books, in various languages, in which references to meteors might be expected. From these sources I have prepared Table I containing 1336 trains which either lasted at least 60 seconds or which, if shorter in duration, showed actual drift. This table, along with Table II which has further data upon 583 of the 1336 mentioned, gives in condensed form the salient facts upon every train. Table II has specific data on heights and drifts, the latter being the original chief aim of this research.

Two men only have published extensively on this subject, Trowbridge in America in 1907-

1911 and Kahlke in 1921 in Germany. The present paper not only contains the hundreds of trains observed since 1921, but by more careful search of old records has perhaps doubled the numbers actually used by the two scientists mentioned in writing their papers. As I do not consider myself competent to attempt a complete physical theory based upon the observed facts, I have contented myself with presenting them in such form that this paper should be fundamental to future studies of currents in the upper atmosphere. The reason for this statement is that it appears to be based upon far the largest existing collection of data on the subject.

The following deductions are of special interest:

- | | | |
|---|------------------|------------------------|
| (A) Night trains | Beginning height | 102 km (51 cases) |
| | End height | 74 km (54 cases) |
| (B) Day trains | Beginning height | 57 km (19 cases) |
| | End height | 30 km (22 cases) |
| (C) Based upon the above values; these velocities were found: | | |
| | Night trains | 175 km/hour (30 cases) |
| | Day trains | 133 km/hour (8 cases) |

Based upon assumed values for heights, these velocities were found:

- | | |
|--------------|------------------------|
| Night trains | 214 km/hour (41 cases) |
| Day trains | 121 km/hour (4 cases) |

In the velocities, where there were two or more values for the same train, the average value was used in the above tabulation.

This paper was finished too late to make a very complete analysis of the directions of drift. In any case this should be done by a trained meteorologist, as it will doubtless be as soon as the data are published. The only striking preponderance of drift that I find from a preliminary study is a considerable one to East for day trains over the Eastern Hemisphere land mass, and a less striking one of drift to West for the night trains over the same area. For North America, the Oceans, and the few from the Southern Hemisphere, each group treated separately, nothing striking is found except a preponderance of night trains drifting to

¹ Aided by a grant from the Penrose Fund of the American Philosophical Society.

the North for America. This is contrary to Kahlke's findings.

The average for the two values, measured and assumed, for night trains is 194 km/hour, for the day trains 127 km/hour. As the mean levels are 88 km and 44 km respectively, it seems to indicate a general increasing wind velocity as we go higher. It will be noted that these means, 88 km and 44 km, represent quite well those for the Kennelly-Heaviside Layer at night and perhaps also in the day.

The most casual study of the data will show at once that the drifts are complex and not simple. The same train will often indicate many superimposed currents of different velocities and very different directions. Incidentally it should be noted that for all trains observed from only one station the drift given is merely a projected drift and not the real one. Only for those trains which were triangulated could the true direction of drift be found, or indeed the true heights of the trains. Some parts of the trains, even their centers, may be at times stationary, while the rest has considerable velocity. Further there is proof in certain cases of components both upwards and downwards, indicating vertical convection. There are also whole trains which show no appreciable distortion or motion, others however in which violent forces seem at work. It must be remembered that the body which causes the train is a meteor, a solid body of from a few inches to a few feet in diameter. This, striking and penetrating our atmosphere, with a velocity of from 15 to 75 km/sec, can only make a cylindrical path of small cross-section, no matter how many miles in length. Yet in less than one minute this path is often defined by a cylindrical glow fully a kilometer in diameter, which in many cases grows even larger. Besides gas diffusion some type of repulsive force is indicated. Again the opposite phenomenon is seen; the ends of the train contract towards the center, apparently, and the whole becomes an elliptical ball of light, which in turn sometimes expands in diameter or merely diffuses away.

Table III, giving monthly totals for all years, shows a great excess for November, August and October, in order of magnitude. The great Leonid showers with some Bielids cause the November maximum, the excellent annual Perseid shower that of August, and the smaller Orionid shower of October gives the excess for that month. Two out of three of these showers are certainly connected with comets, the third probably so. This

would indicate that cometary meteor streams were good breeding grounds for meteors which would produce long-enduring trains. Yet in advance no prediction can be made as to *what* meteor will or will not leave such a train. Take the excellent 1931 Leonid display for example. In this I saw some bright Leonids leave trains persisting up to 10 minutes, yet equally bright ones and of similar color and appearance leaving trains which vanished in from one to two seconds. Why the difference? No one knows.

As said, the stratum contained between 102 and 75 km from the Earth's surface roughly defines the region in which long-enduring night trains are found. For day trains we found the limit 57 and 30 km only. Yet it would be erroneous to believe that we are dealing with totally different phenomena. The best example is the great meteorite of 1933 March 23, our No. 1103, seen over parts of Texas, Oklahoma and New Mexico. This I reported on here in 1935. True this fireball came in twilight, yet we found a continuous train from 100 km to 25 km which lasted fully an hour at upper levels, at least 10 minutes at the lower levels, and which showed all typical train characteristics. We may also refer to our numbers 45, 393, 567, 604, 778 and 1081? as cases in which the strata are overlapped. There are others as numbers 588, 699, 750 and 1264 which would indicate a higher upper limit to the night stratum. Of course, some of these abnormal heights may well be accounted for by errors of observation; it seems impossible that this can explain No. 1103. In any case the debris of the meteor, fine dust and molecules of gas, are present all along the path. Exactly what optical effects the moving mass itself produces upon the atmospheric molecules it actually meets and those it brushes aside, and what further effects are caused by the mixing of the debris mentioned, may in part be deduced or inferred from the tabular data.

It should be said that vast numbers of the brighter meteors leave trains visible one or more seconds. Such trains are not limited to the stratum discussed. The choice of a 60-second duration by me for this paper was purely arbitrary, but I think was made on sound reasoning. How long a train is visible depends upon many factors, such as clearness of sky, absence of moonlight etc. Also the use of a field glass or telescope often prolongs visibility many times. The use of optical aid in the study of trains is there-

fore highly recommended. Meteors themselves appear usually at considerably greater heights than the upper level of the train stratum. They disappear, on an average, about its center. This indicates that meteors which leave long-enduring trains penetrate lower than most. This latter fact would in turn indicate a comparatively larger mass than the average, which would give a better chance for survival. As to slow or great velocity being the deciding factor, we find the very fast moving Leonids often leave fine trains. The number seen in the fine Bielid showers was much smaller but so was the average magnitude of the meteors themselves. The same may be said of the fine Draconid shower on 1933 October 9, when the meteors were both fainter and slower than Leonids. Knowing nothing of the average mass of meteors in the dif-

ferent streams, though I have no reason to believe that they differ to any great extent, there are not data sufficient to say whether the velocity is the decisive factor. The elements present in a given meteor may have much influence.

In closing I desire to emphasize that I have only analyzed my data for certain purposes, largely of an astronomical nature. Indeed the long experience I have had in practical meteor work, covering over 42 years, and my wide acquaintance with others in the same field have given me a special opportunity for carrying this research as far as I have. I now willingly hand on the results to the physicist to supply the necessary theories to explain fully the causes of the phenomena, and to the meteorologist to apply the new data to studies of the upper atmosphere.

TABLE I

The columns are headed as below and the following notes explain their contents.

No.—Serial number, also repeated in Table II.

Date—Astronomical date (old style) which begins 12 hours after civil date, i.e. at noon not midnight.

Hour—Expressed from noon as zero. Local time used when known.

Type—N denotes a train seen at night, T one in twilight, D one in daylight, i.e. with Sun above horizon. It is obvious that some cases are on the borderline and another investigator would classify otherwise.

λ, ϕ —The approximate longitude and latitude of observer(s), or of region over which meteor passed. In latter case the end point would be chosen, if known.

Radiant—Given if known. One or more ? denote increasing uncertainty.

Maximum Magn.—The highest estimated magnitude either in stellar magnitudes or by letters. M designates (full) Moon, S the Sun, Br brilliant, F fireball, B that object burst,—that no information is given as to magnitude. However, in most such cases, except for shower meteor, we may assume F would be entered. x denotes that meteor itself was not seen, only its light and the train that was left.

Duration—Given in minutes and fractions,* denoting the duration was determined using a telescope, field glass etc. This is usually much longer than visibility to unaided eye.

Motion of Train—S denotes spiral, Z-shaped, or serpentine; C curved; R ring-shaped, whole or in part; B ball of light; L cloud-shaped; D that

direction of drift was derived; Z no observed motion, hence zero drift; Y presumed that there was very little drift; K comet-like; E expanded; M definite motion, no direction given; P drawings, diagrams or photographs given; A uncertain whether duration of meteor or train was meant.

References—The usual ones for current journals. 'Greg' and 'Biot' refer to their catalogues. A few books are mentioned by name. Jahr A + G refers to *Jahrbuch für Astronomie und Geophysic* for 1901, which has a table giving partial data as to many trains. In a number of these cases I regret inability to find the original reference. Where the originals were found, this designation was omitted. The latter remark may be repeated as to Greg. After 1900 an increasing number of personal reports has been sent to me or to the American Meteor Society, which I direct. Single reports bear the observer's name. U S N Hy O designates reports to the Hydrographic Office U. S. Navy, largely published in its Bulletin. HC followed by a number denotes the serial number in *Katalog der Bestimmungsgrößen für 611 Bahnen Grosser Meteore*; Wien Ak. Vol. 100, 1925, by von Niessl and Hoffmeister. K followed by a number refers to the serial number in Kahlke's tables in *Meteorschweife und hochastosphärische Windströmungen*; Ann. Hydr. Sept. 1921. The words stone, iron, etc., mean that this type of meteorite was found as a result of the appearance of the fireball mentioned in table.

Note: The 1936 reports of N. Guriev were made at a place named Khodja-Obi-Garm, Varzob district, U.S.S.R. The only place that approximately fitted this name was in $\lambda = 63^\circ$ E $\phi = 36^\circ$ N. This identification may be in error.

NO.	DATE			HOUR	TYPE	λ ϕ		RADIANT α δ	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D			$^{\circ}$ $'$	$^{\circ}$ $'$					
1	-32	10	26	-	N	China			Br	Sev.	R,D	Biot.
2	-12	5	23	16:	N	China			B	90+		Biot.
3	90				N	China			F,B	Sev.	Y	Jour. de Phys., 38,348,1818
4	584	12	-	12:	N	China						C.R., 12,501,1842
5	811	3	30	4:	D	China			Br,B	H S	Z +	Biot.
6	903	3	-	-	-	China			> M,B	3 D	Z + ??	Biot.: near vernal equinox!
7	935	9	21	-	-	32E	28N			?	S	Greg., stone
8	1001	12	14	-	-					Long	S	C.R., 12,506,1842
9	1013	3	16	N ?	-	0	35N		M	15		Greg.
10	1028	5	16	16:	N	China			F,B	Long	L	Biot.
11	1036	5	21	17:	T	45E	33N		S	Long	S	Jour. Osmania Univ., 3,1935
12	1039	4	6	-	-					Long		C.R., 12,506,1842
13	1464	4	5	-	N	China			Br	Long	S	Biot.
14	1488	9	21	22:	D	China			Br	Long	L,S	Biot.
15	1492	9	21	-	N	- W	- N		F	Long		Boston Jour. 1892 Sept. 21
16	1533	10	24	-	N	China		Leonid ?	Br	Long	L	Biot.
17	1626	7	9	13:20	N	E	N		$\frac{1}{2}$ M	15	Z	Arago II, 570
18	1648	1	8	4:	D	12 E	42 N			15		Chladni p. 100
19	1664	8	3	-	-	17 E	47 N		Br	?	C	Wien. Ak., Sb. 37,808,1859: Biot.
20	1676	3	31	-	-				F	1-2	A	Chladni p. 105
21	1683	8	12	9:	N	12 E	51 N		Br	15	Z \pm ?	W. & R. "Metcon", 12,X,21,1733
22	1686	7	19	13:30	N	12 E	52 N		$\frac{1}{2}$ M	7	Z	Greg., C.R. 73,514,1873
23	1688	4	17	2:30	D	9 E	49 N		F	15	M	Chladni p. 105
24	1719	3	19	8:08	N	4 W	51 N	295 + 45	< S	1 +	Z	Phil. Tr. 30,978, 1719
25	1729	4	19	7:	T	6 E	46 N		-	75		Jahr. A. & G. 12, 1901
26	1729	6	2	-	-	8 E	47 N		F	66	M	Chladni p. 109
27	1738	7	13	11:	N	2 E	46 N		$\frac{1}{2}$ M	30	M	Chladni p. 112
28	1741	12	11	1:00	D	2 W	50 N		M	20+	L35° ?	Phil. Tr. 42, 138, 1742: K 1 d
29	1743	10	15	9:30	N	0	52 N		F	20+	D,K	Quetelet Cat.: Am. Jour. Sci. 40,363,1841
30	1745	7	14	8:	T	1 W	52 N		F	61	D,C,P	Phil. Tr. 43,522,1745
31	1746	3	7	20:	D	7 E	51 N		F	30	L	Chladni p. 115
32	1750	6	7	7:	D	1 E	53 N		F	?	L	Greg.
33	1751	5	26	6:50	D	16 E	46 N	60 + 20	B	4 h \pm	S,P	H.C. 166: K2d: iron
34	1753	12	4	3:	D	0	48 N		B	4-5		Chladni p. 116
35	1755	11	27	9:	N	16 E	62 N		M	Long		Greg.
36	1756	1	2	7:	N	6 W	55 N		F,B	16		Greg.: Jahr. A. & G. 12, 1901 (possibly 1755)
37	1761	2	7	8:30	N	2 W	50 N		F	5	M	B.A.A.S. 33,210,1864, and 36,414,1867
38	1761	11	3	6:	N	1 W	51 N		F	15		Greg.
39	1762	11	12	16:45	N	5 E	43 N		B	?		Greg.: Jahr. A. & G., 14,903 gives 1761-11-12: Meteorite
40	1762	12	5	8:45	N	4 W	50 N		M	Sev. ?	C,S	Greg.: E.M., 79,264,1904
41	1763	4	29	2:45	D	2 E	49 N		F	14	K	Greg.: Sirius 34,12,1901: B.A.A.S. 33,210,1864
42	1768	12	22	19:	T	S. Atlantic			B	2	L	B.A.A.S. 36,414,1867; Pogg. An. 129, 174 (Sirius 24,11,1891 and 34,12,1901: A. N. 3030
43	1771	6	3	9:	T	2 E	49 N		X	30	D,K	Chladni p. 127
44	1778	2	-	10:	N	13 E	53 N		M	Long ?	M	Tr. Am. Phil. Soc., 2,173,1786; Olivier notes
45	1779	10	31	6:10	T	83 W	37 N	306 + 37	F	15	S	B.A.A.S. 41,110,1872
46	1783	9	26	-	N	1 W	51 N		Br	3*		Phil. Tr. 74,114 and 219,1784
47	1783	10	4	6:43	N	0	51 N		F	1 $\frac{1}{2}$		B.A.A.S. 29,60,1860
48	1783	10	17	21:15	D	0	50 N		< M,B	1		Greg.
49	1786	9	2	-	-	2 W	51 N			40	B	Wien Ak., Sb. 37,808,1859; B.A.A.S. 29,16, 1860
50	1791	11	11	18:39	N	10 E	52 N		F	< 1?	S,C	Greg.
51	1793	9	10			2 W	55 N		> -2	5		Greg.
52	1794	6	16	7 +	D	11 E	43 N			60+	L	Chladni p. 133, stones
53		6	27	15:55	T	1 W	51 N			3 +	Y,B,P	B.A.A.S. 41,110,1872
54	1798	7	28	2:30	D	0	53 N		F,B	30	L	Greg.: Jahr. A. & G. 12, 901
55		10	8	16:24	N	12 E	51 N			1 \pm	D,C,P	"Die Sternschnuppen" p.348,1839
56	1803	10	10	8:06	N	14 W	38 N		Br B	60	Y	Wien Ak. 62 II, 863,1870

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
57	1805	10	23	7:30	N	7 E	53 N	c c	F	20	D, C, S	(Phys. Worterbuch 4, 220, 1827; H.C., 406; K; Gilbert Ann. 23, 106
58	1810	1	2	12:30	N	6 E	46 N		F	15	S	Greg.: Jahr. A. & G. 12, 1901
59	1811	5	15	8:35	T	3 E	47 N		F	10	S, E	Phil. Mag. 64, 118, 1824
60	1812	8	9	-	-	1 W	47 N		-	?	L	Jahr. A. & G. 12, 1901
61		8	23	9:	N	5 E	52 N		F	15		Chladni p. 154
62	1813	11	10	6:40	N	1 W	55 N		X	6	Y	Chladni p. 156; Ann. of Philos. 2, 456, 1813
63	1814	9	5	0:	D	1 E	44 N		F	Long	D, L, L	Ann. de Chemie. 9, 28, 1814; Stone
64		10	18 ?	10:	N	12 E	51 N		-	Many		(Jahr. A. & G. 12, 1901 (possibly Oct. 14, Greg.) Wien Ak., 37, 811, 1859
65	1815	5	10	10:30	N ?				F	Sev.	R	Chladni p. 158
66		7	2	P.M.	-	12 E	51 N		-	26	K	Sirius 34, 11, 1901
67	1817	4	10	10:		14 E	50 N		B	1+		Chladni p. 161
68	1818	2	15	6:30	N	1 E	45 N		B	30	D, L	B.S.A.F. 12, 268, 1904
69		8	3	11:15	N	0	51 N		F	1	Z, K	Sirius 34, 12, 1901; Greg.
70		10	31	8:30	N ?	26 E	45 N		F	5		B.A.A.S. 30, 66, 1860; aerolite
71	1819	5	5	0:30	D	2 E	57 N		B	Long	L	Greg.: Phil. Mag. 54, 75, 1819
72		11	13	-	-	72 W	19 N		F	18		Greg.
73	1821	6	15	3:00	D	5 E	44 N		B	15	Z	C.R. 89, 918, 1879; K 3d; stone
74		9	20	15:43	N	31 E	29 N		F	2		Pog. Annalen 612, 1874; B.A.A.S. 43, 190, 1874
75	1822	3	9	10:00	N	77 W	42 N	257 + 40	B, M	10	C	Am. Jour. Sci. 6, 318, 1823; Phil. Mag. 64, 118, 1824; H.C. 86
76		3	16	10:05	N	78 W	37 N		F, B	Sev.		Arago. II, 570, Phil. Mag. 59, 399, 1822
77		6	3	8:15	T	0	47 N		F	15	D, S	Gil. Annalen 71, 345, 1822; K 4 d; stone
78		8	6	-	-	0	50 N		F	5	S	Phil. Mag. 64, 119, 1824
79		8	11	-	-	8 E	47 N		F	3		Greg.
80		9	1	-	-	77 W	18 N		F, B	Sev.		Greg.
81		11	15	7:58	N	10 E	54 N		B	1+	Y	A.N. I, 449, 1823
82	1823	8	7	4:30	D	70 W	44 N		Br	?	B	Am. Jour. Sci. 7, 170, 1823; stone
83		11	9	6:45	N	14 E	50 N		x	2 -	D, K	A. N. I, 468, 1824
84	1825	11	14	-	-	3 W	56 N			2	K	Greg.
85		11	22	-	N	88 E	25 N		F	2.5	K	B.A.A.S. 19, 120, 1850
86		12	2	-	-	88 E	25 N		Br	5		B.A.A.S. 20, 43, 1851
87	1826	3	31	9:	N	73 W	41 N		B	1		Am. Jour. Sci. 11, 184, 1826
88	1827	12	11	-	-	8 E	49 N			75	K	V. Boguslawski; Sirius 34, 12, 1901
89	29	9	26	11:48	N	7 E	51 N		F	13	K, C	A. N. 8, 15+ 159, 1831
90	31	11	12	16:00	N	5 E	47 N	Leonid	F	6		Quetelet 39, 1839; Nat. 53, 7, 1895
91	32	10	20	10:	N	3 W	52 N	Orionid ?	1	Sev ?	Y	B.A.A.S. 21, 182, 1852
92	33	11	12	-	N	74 W	41 N	Leonid	?	15	C	Trans. Am. Phil. Soc. N.S. 7, 271
93		11	12	15:00	N	80 W	36 N	Leonid	>M	30 \pm	S, D, P	Am. Jour. Sci. 25, 378, 1834
94		11	12	-	N	77 W	38 N	Leonid ??	?	10		Am. Jour. Sci. 25, 390, 1834
95		11	12	16:00	N	81 W	41 N	Leonid ??	F	75	C, D	Am. Jour. Sci. 25, 391, 1834
96		11	12	-	N	77 W	38 N	Leonid ??	?	2.3		Am. Jour. Sci. 25, 390, 1834
97		11	12	16: ?	N	80 W	40 N	Leonid ??	F	15 -	L, D	Am. Jour. Sci. 25, 391, 1834
98		11	12	17: ?	N	80 W	40 N	Leonid ??	?		I	Am. Jour. Sci. 25, 391, 1874
99		11	12	17:15	N	78 W	43 N	Leonid ??	F	3	C	Am. Jour. Sci. 26, 338, 1834
100		11	12	17:30	N	77 W	39 N	Leonid	?	4	L, S	Am. Jour. Sci. 25, 375, 1834
101 a		11	12	17:40	N	81 W	39 N	Leonid ?	- 5	15	C	Am. Jour. Sci. 26, 87, 1834) same
101 b		11	12	-	N	83 W	40 N			10	D	Am. Jour. Sci. 26, 338, 1834) meteor?
102		11	12	17:45	N	73 W	41 N	Leonid	B	15 -	S, D	Am. Jour. Sci. 26, 156, 1834
103		12	8	-	N	12 E	52 N			?	L, P	"Die Sternschnuppen" 348, 1839
104	1834	7	4	9:15	T	0	52 N		F	60 +		B.A.A.S. 21, 183, 1852
105		9	29	7:15	T	0	53 N		F	2.5	C, P	B.A.A.S. 21, 183, 1852
106	1835	11	14	-	-	18 E	34 S		-	20		Jahr. A. & G. 12, 1901
107		12	12	12:	N	12 E	52 N		Br	2		Greg.
108	1836	8	20	4:	D	90 W	40 N		$\frac{1}{2}$ M, B	15	L	Am. Jour. Sci. 33, 402, 1838
109		11	14	--	-	24 E	38 N		-	5	K	Sirius 34, 12, 1901
110		11	14	-	-	12 E	47 N		-	5		Jahr. A. & G. 12, 1901*
111	1837	8	5	7:30	T	73 W	41 N		S, B	Sev.		Am. Jour. Sci. 33, 200, 1838
112	1838	1	2	7:	N	17 E	51 N		Br	2		Greg; meteorite
113		3	17			0	53 N		Br	10	K	Greg.

NO.	DATE			HOUR	TYPE	λ ϕ	RADIANT α δ	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D								
114		8	18			9 E 49 N			4		Greg.
115		11	13	17:	N	73 W 41 N	Leonid	B	9	D,E	Am. Jour. Sci. 35,369,1839
116		11	-	7:30	N	78 E 8 N		M	20+	C,L,Z	B.A.A.S. 20,43,1851
117	1839	8	7			42 W 44 N		F	1		Greg.
118		8	26	9:	N	20 E 41 N		Br	20	S	Am. Jour. Sci. 39,381,1840
119	1840	1	8	7:50	N	10 E 54 N		B, $\frac{1}{2}$ M	1	K	A. N. 18,54,1841
120		5	12	15:	N	72 W 41 N		B,M	4 -		Am. Jour. Sci. 39,382,1840
121		7	30	-	-	16 E 48 N		B	15	C	Wien Ak. 37,811,1859
122		8	10	-	-	6 E 51 N		-	1.5		Jahr. A. & G. 12, 1901
123	1841	3	8	-	-	3 E 40 N		B	2		Greg.
124		8	10	-	-	6 E 51 N			1.5		Wien Ak. 37,811,1859
125		9	8	9:53	N	2 E 47 N		B	1.2		C.R. 13,637,1841
126		12	5	6:45	N	17 E 50 N		B,M	1		Greg.
127	1842	4	10	16:00	N	81 E 24 N		F	8+	D,C	B.A.A.S. 19,121,1850; 21,238
128		7	11	9:10	N	0 50 N		F	3.5	D,R	C.R. 15,127,1842
129		8	5	8:20	T	17 E 51 N		B	Long	D,L	Greg.
130		11	11	14:34	N	10 E 45 N		- 5,B	1.5	Y	Met.Mag. 1,325,1842-3
131	1843	3	7	8:48	N	10 E 52 N		F	1+		A.N. 20,315,1843
132		6	21	-	-	3 E 40 N		M	1		Greg.
133		11	10	5:	D	20 E 45 N		X	4 -	L,M	B.A.A.S. 17,5,1848 (possibly Nov. 12): meteorite
134	1844	9	3	16:00	T	75 E 20 N		F	20	D	B.A.A.S. 21,238,1852
135		9	10	-	-	4 E 51 N		F	2		Greg.
136	1845	6	18	8:	T	31 E 37 N		>M	30+	D,L	B.A.A.S. 39,30,1861: K 6 d
137		7	2	14:	T	12 E 51 N		F	26	C,M	Sirius 34,12,1901: Wochen 2,226,1859
138		10	24	12:00	N	7 E 51 N		- 4	5 -	D,C,S	(Schmidt.. '10 Years..', 93,1852 (Wien Ak. 56, II, 503,1867: K 2 (B.A.A.S. 29,16,1860
139	1846	6	20	8:30	T	4 E 37 N		Br	1		Greg.
140		6	21	9:30	N	9 E 49 N		-4,8	15		Wien Ak. Sb. 56,II,504,1867
141		8	24	10:30	N	1 E 45 N		Br	4 -		Greg.
142		9	25	10:	N	0 53 N		- 5	?	S	Phil.Mag.30,4:31,368 and Ap.4
143		10	17	6:15	T	9 E 50 N		- 3	8		C.R. 46,985,1858
144		10	24	6:45	N	17 E 51 N		B	2	L	Greg.
145		11	9	7:30	N	5 E 47 N		Br,B	15	L,L	C.R. 23,985,1846
146		11	11			71 W 42 N		M,B	5		Greg.
147		11	19	P.M.	N	1 W 49 N		>- 2	20	Z	C.R. 23,986,1846
148	1847	1	10	5:00	T	16 E 48 N		$\frac{1}{2}$ M	10	S,M,P	Wien Ak.35,384: 37,811,1859
149		5	26	-	-	1 W 52 N		-	12		Greg.
150		7	13	15:45	T	13 E 52 N		F,B	Some	L,M	Pogg. Annalin 72,170,1847: iron
151		8	10	-	-	2 E 49 N		Br	9	L	Greg.: Jahr. A. & G. 12, 1901 (possibly Aug. 9)
152		8	11	9:53	N	7 E 53 N		Br	1.5+	C	Wochen 1,356,1847
153		10	30	7:	T	73 E 19 N		Br,B	15 ?		Wien Ak. 37,811,1859
154		11	11	-	-	83 E 21 N		B	10		Greg. (possibly Nov. 10):
155		11	20	-	-	1 W 52 N		Br	7+	Y	Wien Ak. 37,872,1859
156		12	8	11:11	N	6 E 51 N	Geminid	1	2 -	E	Greg. Heis '43 Years, etc.' 4, No. 84
157		12	11	8:30	N	70 W 45 N		$\frac{2}{3}$ M	1	Z	Smithsonian Rep. 324,1857
158	1848	1	20	-	-	74 W 41 N		F	12		Greg.
159		3	29	-	-	17 E 48 N		M	30	C,L	Greg.
160		9	4	8:59	N	0 50 N		<M,8	3-	Z	B.A.A.S. 18,14,1849: C.R. 73,513,1871
161	1849	8	9	9:	N	3 E 40 N	Perseid ?	-5	7		B.A.A.S. 20,4+38,1851
162		8	25	10:	N	2 W 53 N		-5	Long		B.A.A.S. 19,104,1850
163		11	5	6:20	N	1 W 53 N	64 + 18	-3	5	S,P	(B.A.A.S. 19,94 + 104, + 106, (1850: HC 427: Phil.Mag.36,381, (1850
164		11	7	-	-	74 E 18 N		B	2		Greg.
165		11	12	16:	N	12 E 54 N		F,B	15		Greg: Jahr. A. & G. 12, 1901
166		11	13	-	-	15 E 32 N		B	90		Proc.Am.Phil.Soc. 17,340,1878:
167		12	4	11:40	N	1 W 53 N		-5	8		Greg. stones
168		12	19	5:10	N	1 W 53 N		-5	2.5		B.A.A.S. 19,94,1950

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
169	1850	1	1	15:45	N	6 E 51 N			M, B	2 -		B.A.A.S. 29, 102, 1860; C.R. 73, 513, 1871
170		2	5	6:50	N	1 E 51 N			$\frac{1}{2}$ M, B	3 +	Z	B.A.A.S. 20, 6, 1851
171		2	11	10:45	N	2 W 55 N			B	5		Phil. Mag. 36, 221 + 249, 1850;
172		2	13	9:35	N	1 W 53 N			$\frac{1}{2}$ M	1.5		Greg.
173		6	5	9:15	T	5 E 49 N			< M, B	Sev.		A.M. 35, 285, 1853
174		7	28	-		8 E 52 N			F	10		Greg.
175		9	30	8:54	N	71 W 42 N			B	75*	C, D, S	B.A.A.S. 24, 95, 1855
176		11	6	7:00	N	73 E 18 N			B	20*	K	B.A.A.S. 20, 44, 1851; 19, 238, 1852
177	1851	4	17	8:	N	7 E 51 N			M, B	3		Wien Ak. 37, 804, 1859; stone
178		4	20	10:	N	80 E 26 N		Lyrid ?		1 +		B.A.A.S. 20, 51, 1851
179		5	2	10:	N	80 E 13 N		Sp.	X	1 +		B.A.A.S. 21, 228, 1852
180		5	22	10:15	N	80 E 13 N			Br	2		B.A.A.S. 21, 228, 1852
181		6	20	11:30	N	2 W 51 N			F	3.5	Z ??	B.A.A.S. 20, 36, 1851
182		6	22	9:30	T	6 W 55 N			M, B	10	E, Y, D	B.A.A.S. 20, 36, 1851
183		11	5	5:30	T	5 W 40 N			B, $\frac{1}{2}$ M	20	L	B.A.A.S. 21, 202, 1852; stones
184	1852	8	12	-		3 W 51 N			M	2	Z	Greg.
185		10	5	9:15	N	5 E 50 N			Br	Long		B.A.A.S. 36, 417, 1867; 21, 212, 1852 Cosmos, Dec. 1852
186		11	24	-		2 E 49 N			F, B	5		Greg.
187	1853	8	9	-	-	17 E 50 N			-	30		Jahr. A. & G. 12, 1901
188		8	26	-		17 E 53 N			Br	10		Greg.
189		9	12	-		5 E 46 N			-5	6		Greg.
190		10	26	14:	N	17 E 53 N			-4	10	S	Wien Ak. Sb. 37, 809, 1859;
191		10	28	3:57	D	0 53 N		261 + 49	$\frac{1}{2}$ S	5	E	B.A.A.S. 23, 414, 1854; H.C. 416
192		12	11	9	N	12 E 51 N			Br	15	K	Sirius 34, 11, 1901
193	1854	4	1			14 E 52 N				3		Wien Ak. 37, 812, 1859
194		8	1	12:34	N	10 E 52 N		Perseid	Br, B	8.3 *	D, S, P	Wien Ak. 37, 809, 1859; Heis 61; K3
195		8	1	14:04	N	10 E 52 N		Perseid	Br	2.5 *	D, S	Heis 61; K4, A.M. 39, 116 + 118, 1855
196		10	17	-		10 E 54 N			B	Long		Jahr. A. & G. 12, 1901
197		11	16	23:	D	7 E 53 N			F, B	Long		Wien Ak. 37, 811, 1859; Greg.
198	1855	1	7	4:45	T	0 53 N		Quad. ?	Br	15 -	D, C, E, P	B.A.A.S. 25, 61, 1856
199		12	10	-	-	13 E 56 N			-	15		Jahr. A. & G. 12, 1901
200		12	18	18:13	N	0 53 N			S	10	D, R, P	B.A.A.S. 25, 61, 1856
201	1856	1	7	4:52	T	1 W 51 N		350 + 33	< M	18	D, C	(B.A.A.S. 25, 54 + 60, 1856; 134 - 140, 1857; H.C. 6; K7d M.M. 16, 161, 1856
202		7	8	6:	D	87 W 33 N		157 + 15	Br, B	15	S	Am. Jour. Sci. 11, 22, 248 + 23, 287 H.C. 214
203		7	30	9:48	N	2 E 49 N			Br	4	Z	C.R. 43, 257, 1856
204		8	10	9:07	T	0 53 N		Perseid ??	-3	1		B.A.A.S. 27, 140, 1858
205		10	29	6:15	N	14 E 46 N			$\frac{1}{2}$ M	30	D, C	Unterh. Astr. 375, 1856; Greg.
206	1857	4	11	9:	N	94 W 46 N			> M	10	Y	Greg.
207		7	20	-		0 52 N				5	M	Greg.
208		11	23	11:38	N	0 53 N			-3	5	Y	B.A.A.S. 27, 148, 1858
209	1858	7	11	11:10	N	11 E 54 N			-5	3-		Wochen. 1, 297, 1858
210		8	9	11:59	N	140 E 36 N		Perseid ??	B	1	Z	B.A.A.S. 34, 60, 1865; 36, 417, 1867
211		8	12	-		2 E 49 N			-5, B	3		Greg.
212		8	26	8:45	N	13 E 50 N			-4	1	Y	Wochen. 2, 221, 1859
213		9	10	10:20	N	7 E 50 N			$\frac{1}{2}$ M	Long	B, B	Wochen. 1, 415, 1858
214		11	12	14:45	N	7 E 51 N			B	10 -	K, Z, S	Wochen. 2, 225, 1859
215		12	5	5:	T	50 E 13 N			Br	15	D, E, P	B.A.A.S. 28, 86 + 91, 1859
216		8	9	14:56	T	24 E 38 N		Perseid	0	3.7*	D, P	Wien Ak. 56, II, 509, 1867
217	1859	8	9	15:56	T	24 E 38 N				2.8*	M, P	Wien Ak. 37, 810, 1859
218		8	9			24 E 38 N				2.3		Wien Ak. 37, 812, 1859
219		8	10	19:20	D	74 W 43 N			Br	Long	L, Z	Am. Jour. Sci. II 28, 300, 1859
220		8	17			12 E 51 N			Br	Long		Greg.
221		8	20	6:40	D	118 E 24 N			Br	10	S	B.A.A.S. 33, 210, 1864
222		10	18	9:37	N	24 E 38 N			-2	6 *		Wien Ak. 56 II, 509, 1867
223		10	27	9:32	N	24 E 38 N			-3	5 + *	M, P, S	(Wien Ak. 44, II, 227, 1862; Schmidt 227, Wien Ak. 56, II, 509, 1867
224		11	8	17:30	N	0 53 N			Br	10	L, E	B.A.A.S. 29, 8, 1860
225		11	14	21:30	D	75 W 39 N		243 + 30	S, B	2	D, S	Am. Jour. Sci. 29, 137 + 298; 30, 186 H.C. 454

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	δ	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D										
226	1860	1	24	5:05	T	6 E 51 N				-4	15	S, B	Wochen. 4, 61, 1861
227		2	23	9:46	N	24 E 38 N				-3	1.7		Wien Ak. 56, II, 510, 1867
228		8	9	10:35	N	24 E 38 N				1	2 *	C, P, D	Wien Ak. 44, II, 227, 1861
229		8	10	15:10	N	24 E 38 N		Perseid		-3	1 + *	D, P	Wien Ak. 44, II, 227, 1861; 56, II, 510, 1867
230	1861	3	3	21:30	D	144 E 38 S				$\frac{1}{2}$ M, B	20		B.A.A.S., 35, 127, 1866 + 36, 419, 1867
231		5	17	14:	N	145 E 38 S				> -3	1		Wochen. 13, 346, 1870
232		7	16	11:30	N	0 51 N		32 + 23		M	5	D, C	B.A.A.S. 31, 10, 1861; 5+77, 1862; H.C. 224: K5
233		7	25	11:02	N	13 E 53 N				M	23		Sirius 29, 9, 1901
234		7	29	-	-	22 E 39 N				-	3		Jahr. A. & G. 12, 1901
235		8	9	13:38	N	24 E 38 N		Perseid		-1	3 *	D, P	Wien Ak. 44, II, 227, 1861
236		8	10	9:20	N	3 W 43 N		Perseid??		Br	4	Y	B.A.A.S. 30, 16, 1861
237		8	12	12:25	N	24 E 38 N		Perseid		-1	1 *	Z	Wien Ak. 44, II, 228, 1861
238		10	4	?	?	73 W 41 N				F	2	S	B.A.A.S. 36, 419, 1867
239		11	15	10:30	N	91 W 42 N				F, B	Sev.		B.A.A.S. 46, 102, 1877
240	1862	1	9	11:30	N	14 E 50 N				< M	10	A	Wochen. 15, 136, 1862
241		2	7	5: ?	T	17 E 49 N				F	10		B.A.A.S. 36, 420, 1867
242		4	23	10:03	N	24 E 38 N				M	30 *		Wien Ak. 56, II, 511, 1867; B.A.A.S. 36, 421, 1867
243		4	25	8:20	N	147 E 43 S		Sp.		> M	10	D	B.A.A.S. 36, 291 + 374, 1867
244		7	28	2: ?	D	9 E 46 N				F	15		B.A.A.S. 36, 421, 1867
245		9	19	10:14	N	0 51 N		22 + 16		M	11	Z, S	B.A.A.S. 31, 73, 1862; HC 353: Proc. B.M.S. 1, 263, 1862
246		9	27	-	-	14 E 41 N				-	Many		Jahr. A. & G. 12, 1901
247		10	26	7:45	N	3 W 52 N		Sp.		Br	3	D, C	B.A.A.S. 32, 226, 1863
248	1863	7	19	8:12	T	2 W 52 N		310 -12		B	23	S	B.A.A.S. 32, 262, 1863; H.C. 229
249		8	9	9:48	N	8 E 52 N		Sp.		1	2.2 *		B.A.A.S. 32, 331, 1863; Heis 99
250		8	10	9:30	N	13 E 45 N		27 + 52		$\frac{1}{2}$ M	4	S	B.A.A.S. 33, 274, 1864; 33, 90, 1864
251		8	10	9:24	N	0 51 N		Perseid		-4	4.5 *	S	B.A.A.S. 32, 276, 1864
252		8	10	9:31	N	8 E 52 N		Perseid		-4	0.9 *		B.A.A.S. 33, 331, 1864; Heis 101, Wochen. 6, 259, 1863
253		8	10	9:45	N	12 E 46 N		Perseid		M ?	10	D, S	Wien Ak. 48, II, 309, 1863
254		8	10	9:51	N	8 E 52 N				-3	0.4 *		B.A.A.S. 33, 331, 1863
255		8	10	10:38	N	8 E 52 N		Sp.		1	1.3 *	S	B.A.A.S. 32, 331, 1864, Heis 102
256		8	10	10:46	N	0 51 N		Perseid ?		-5	4.5 *	R, P	B.A.A.S. 33, 296 + 333, 1864
257		8	10	11:08	*	8 E 52 N				-3	0.7 *		B.A.A.S. 33, 331, 1864
258		8	10	12:12	N	8 E 52 N		Perseid		1	2.8 *	R, L	B.A.A.S. 33, 331, 1864; Wochen. 6, 323, 1863
259		8	10	12:39	N	20 E 50 N		Perseid		Br	5	C, B, B	Wochen. 6, 373, 1863
260		8	10	12:52	N	8 E 52 N		Perseid		-3	1 *	C, D	B.A.A.S. 33, 331, 1864; Wochen. 6, 259, 1863
261		8	10			24 E 38 N					13		Jahr. A. & G. 12, 1901
262		8	10			20 E 50 N					Many		Jahr. A. & G. 12, 1901
263		8	21	10:35	N	24 E 38 N				M	5 *	Z	Wien Ak. 56, II, 512, 1867; Wochen. 6, 316, 1863
264		9	12	8:40	N	24 E 38 N		Perseid		-3	90 *	D	Wien Ak. 56, II, 512, 1867; Wochen. 6, 316, 1863
265		10	15	10:00	N	1 W 53 N		80 + 23		-4	10	K	B.A.A.S. 33, 8: H.C. 393
266		10	18	14:55	N	24 E 38 N		102 -29		Br	10 *	D, R, P	Wien Ak. 48, II, 551, 1863; 56, II, 512, 1867; Wochen. 6, 375, 1863
267		11	6	5:42	N	24 E 38 N				-3	7 *		Wien Ak. 56, II, 513, 1867
268		11	13	13:32	N	24 E 38 N				-3	5 *		Wien Ak. 56, II, 513, 1867
269		11	13	13:38	N	24 E 38 N				-4	5 *		Wien Ak. 56, II, 513, 1867
270	1863	11	13	14:02	N	24 E 38 N				-3	8 *		Wien Ak. 56, II, 513, 1867
271		11	13	15:05	N	24 E 38 N				-3	30 *		Wien Ak. 56, II, 513, 1867
272		11	13	15:38	N	24 E 38 N				-4	25 *		Wien Ak. 56, II, 513, 1867
273		11	13	16:47	N	24 E 38 N				-4	9 *		Wien Ak. 56, II, 513, 1867
274	1864	2	22	9:	N	38 E 58 N				F	Long	Y	B.A.A.S. 36, 425, 1867
275		5	14	8:00	T	2 E 44 N		86 + 24		M +	30	Y	B.A.A.S. 33, 45, 1864; H.C. 155; C.R. 58, 1066, Bruun 15, 143, 1879; stones
276		7	29	11:23	N	22 E 39 N				-3	3 *		Wien Ak. 56, II, 514, 1867
277		8	2	8:30	N	22 E 39 N				-3	3 *		Wien Ak. 56, II, 514, 1867
278		8	2	12:30	N	22 E 39 N				-4	10.1 *		Wien Ak. 56, II, 514, 1867

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	δ	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D										
279	1864	8	10	6:41	D	24 E 38 N	132+22	Br	16 *	L			Wien Ak. 50, II, 455, 1864; H.C. 280
280		8	15	12:40	N	9 E 47 N		F	Sev.	M			B.A.A.S. 34, 62, 1865; Astr. Reg. 3 11, 1865
281		8	22	9:08	N	22 E 39 N		-4	9 *				Wien Ak. 56, II, 499, 1867
282		9	8	3:	D	14 E 37 N		8	60				B.A.A.S. 36, 427, 1867
283		9	20	16:04	N	22 E 38 N		Br	10				Wien Ak. 56, II, 514, 1867
284		9	24	0:20	D	4 E 44 N	334+50	8	Sev.	D, R			C.R. 59, 573, 605, 1864; H.C. 360; B.A.A.S. 36, 427, 1867
285		11	11	5:36	T	2 E 44 N	55+21	>M	5	E			C.R. 59, 831, 1864; H.C. 434; B.A.A.S. 49, 44, 1880
286	1865	2	15	6:	N	8 E 51 N	279+60	-4	15	S, G			Wochen. 8, 79, 95, 1865; H.C. 60
287		2	17	5:30	T	5 E 51 N		-4	10				Wochen. 9, 367, 1866; B.A.A.S. 34, 88, 1865
288		7	25	11:12	N	24 E 38 N		-4	10 *				Wien Ak. 56, II, 515, 1867
289		7	27	11:09	N	24 E 38 N		-4	21 *				Wien Ak. 56, II, 515, 1867
290		10	18	14:54	N	24 E 38 N		-4	16 *				Wien Ak. 56, II, 516, 1867
291		11	12	16:00	N	73 W 41 N	Leonid ?	Br, B	1 +	D, C			Am. Jour. Sci. II, 41, 58, 1866; K1
292		11	12	16:00	N	73 W 41 N	Leonid ?	Br	Sev. ?	D			Am. Jour. Sci. II, 41, 58, 1866; K2
293		11	12	17:07	N	0 53 N	Leonid	2/3 M	1	Y			B.A.A.S. 35, 58, 1866; 36, 429, 1867
294		11	13	12:48	N	4 E 52 N	Leonid ?	Br	36 *	D, P			Pop. Sci. Mon. 79, 191, 1911 etc.; K6
295		12	24	17:30	N	10 E 54 N		Br, B	3	Z			Wochen. 9, 8, 1866
296	1866	1	12	14:48	N	8 E 45 N		Br	6	D, B, E			Bol. Met. Oss. Torino Jan. 1866
297		6	9	4:55	D	14 E 49 N	170 + 55	8	30+	L, P			Wien Ak. 54, II, 200, 1866; H.C. 189; stones
298		6	19	23:00	D	2 E 47 N	200 + 54	1/3 M, 8	15	Y			B.A.A.S. 35, 104 + 128, 1866; 36, 430, 1867; H.C. 202
299		7	17	9:20	T	10 E 60 N		1/3 M	12	D, S, P			Backhouse letter; B.A.A.S. 36, 430, 1867
300		8	9	11:48	N	24 E 38 N		-4	10.1 *				Wien Ak. 56, II, 517, 1867
301		10	18	15:	N	1 E 51 N	Orionid	F	5	C			B.A.A.S. 36, 294 + 382, 1867
302		11	12	12:30	N	3 W 51 N	Leonid ?	F	45	M, L, S			B.A.A.S. 42, 370, 1873
303		11	12	14:14	N	0 53 N	Leonid	-	15	D			Obs. 20. 273. 1897: K 7
304		11	13	p.m.	N ?	75 E 19 N		-	5	D			Am. Jour. Sci. TT, 43, 276, 1867 (twilight?) K8d
305		11	13	-	N	13 E 53 N	Leonid ??	Br	Sev.	M			Sirius 18, 225-9, 1890
306		11	13	12:10	N	0 52 N		Br	12				B.A.A.S. 36, 306, 1867
307		11	13	-	N	0 52 N		?	0.6 *	C, P			B.A.A.S. 36, 405, 1867
308		11	13	-	N	0 52 N		?	0.7 *	S, P			B.A.A.S. 36, 405, 1867
309		11	13	12:33	N	4 W 56 N	Leonid	-3	5	D, C			B.A.A.S. 36, 306, 1867; K 8
310		11	13	12:40	N	4 W 56 N	Leonid	-5	8.2	D, C			B.A.A.S. 36, 306 + 372, 1867; Phil. Mag. 33, 83, 1867; K9
311		11	13	13:07	N	0 52 N	Leonid	Br	10 *	D, C			B.A.A.S. 36, 308, 1867; K 10
312		11	13	13:08	N	3 W 52 N	Leonid	-4	14	D, S, P			B.A.A.S. 36, 308, 313 and Ap. 1867; K 11
313		11	13	13:12	N	2 W 51 N	Leonid	Br	6	D, L			Denning letter; B.A.A.S. 36, 310, 1867
314		11	13	13:20	N	0 51 N		-5	2				B.A.A.S. 36, 310, 1867
315		11	13	13:28	N	3 W 51 N	Leonid ??	1/3 M	3+	C, B			B.A.A.S. 36, 310, 1867; Met. Mag. 1, 93, 1866
316		11	13	13:30	N	24 E 38 N		-4	2				Wien Ak. 56, II, 499, 1857
317		11	13	13:45	N	0 51 N	Leonid	Br	3	Y			B.A.A.S. 36, 313, 1867
318a		11	13	13:24	N	0 52 N		-1 ?	4+	B			B.A.A.S. 36, 310, 1867) same
318b		11	13	13:00	N	6 W 53 N	Leonid ?	Br	11	C, R			Met. Mag. 1, 109, 1866) meteor?
319		11	13	13:50	N	2 W 51 N	Leonid	Br	9 *	D, C			B.A.A.S. 36, 406, 1867; K 12
320		11	13	14:10	N	1 E 51 N	Leonid	-4	4	M, B			B.A.A.S. 36, 312, 1867
321		11	13	14:11	N	73 W 42 N	Leonid	Br	9	D, C, E			Am. Jour. Sci. II, 43, 86, 1867; K 3
322a		11	13	14:12	N	1 W 53 N	Leonid	?	3	D			B.A.A.S. 36, 313, 1867) same
322b		11	13	14:12	N	1 E 51 N	Leonid	-2	6	D, C, P			B.A.A.S. 36, 313, 1867) meteor ??
323a		11	13	14:14	N	4 W 56 N	Leonid	-4	5.8	D, L			B.A.A.S. 36, 314, 1867; K 14) same
323b		11	13	14:15	N	3 W 56 N	Leonid	Br	1	Y			B.A.A.S. 36, 314, 1867) meteor?
324a		11	13	14:16	N	0 51 N	Leonid	8, -3	1.5	Y			B.A.A.S. 36, 314, 1867; Gr. Obs. 1866, 298 No. 54
324b		11	13	14:16	N	2 W 52 N	Leonid	-5	2				B.A.A.S. 36, 404, 1867) meteor?
325a		11	13	14:20	N	1 E 51 N	Leonid	-5	2.8	D, Y			B.A.A.S. 36, 314, 1867) same
325b		11	13	14:21	N	N	Leonid	-3	2				B.A.A.S. 36, 377, 1867) meteor?
326		11	13	14:40	N	3 W 56 N	Leonid	-5	15	D, P			B.A.A.S. 36, 373, 1867; etc., K 16

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT	MAX. MAGN.	DURATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
327		11	13	15:06	N	0	51 N	Leonid ???	Br	Many	S	B.A.A.S. 36,319 + 407, 1867
328		11	13	15:47	N	2	W 55 N	Leonid		8		Denning: B.A.A.S. 36,370, 1867 ?
329		11	13	16:18	N	24	E 38 N	Leonid	Br	51+	L,C	Wien Ak. 54, II, 775, 779, 1866; 56, II, 502, 1867
330		11	13	16:31	N	24	E 38 N		-3	7		Wien Ak. 56, II, 499, 1867
331		11	13	16:56	N	24	E 38 N		-4	13		Wien Ak. 56, II, 499, 1867
332		11	13	17:05	N	24	E 38 N		-3	7		Wien Ak. 56, II, 499, 1867
333		11	13	18:40	N	1	W 54 N	Sp.	1	1.5		B.A.A.S. 36,318, 1867
334	1867	6	11	8:11	T	2	E 46 N	86 + 44	<M	60 *	D,E,P,S	B.A.A.S. 36,378, 1867; H.C. 195; C.R. 64, 1304: K 9 d
335		7	4	11:58	N	24	E 38 N		-4	5 *		Wien Ak. 56, II, 520, 1867
336		8	10	14:04	N	11	E 45 N	Sp ?	-3	3	M,P	B.A.A.S. 37,348, 1868 Met. Ital. Sup. 1867
337		8	10	14:23	N	24	E 38 N		-2	4 *		Wien Ak. 56, II, 521, 1867
338		8	10	14:51	N	24	E 38 N		-3	10 *		Wien Ak. 56, II, 521, 1867
339		8	11	-	-	15	E 50 N		-	5		Jahr. A. & G. 12, 1901
340		10	3	10:30	N	7	E 51 N		Br	8	S,B	Wochen. 10, 373, 1867
341		11	13	13:57	N	72	W 44 N	Leonid	-5	6	C	Am. Jour. Sci. 2,45,255, 1868; K4
342		11	13	14:51	N	92	W 42 N	Leonid		4	D	Am. Jour. Sci. 2,45,227, 1868; K5
343		11	13	14:56	N	92	W 42 N	Leonid		3	D	Am. Jour. Sci. 2,45,231, 1868; P.A. 44, 562, 1936; K6
344		11	13	15:03	N	92	W 42 N	Leonid ?		2	D	Am. Jour. Sci. 2,45,231, 1868; P.A. 44, 562, 1936; K7
345		11	13	15:08	N	92	W 42 N	Leonid ??		?	D,C	Am. Jour. Sci. 2,45,231, 1868; P.A. 44, 562, 1936; K8
346		11	13	16:00	N	73	W 41 N			4	D	Am. Jour. Sci. 2,45,81, 1868; K 10
347		11	13	16:01	N	92	W 42 N	Leonid ??		?	D	Am. Jour. Sci. 2,45,231, 1868; P.A. 44, 562, 1936; K 9
348		11	13	16:07	N	77	W 39 N	Leonid ?		5	D,L	U.S. Naval Observatory: K 11
349		11	13	16:18	N	74	W 43 N	Leonid		1	B,Y	Proc. B.M.S. 4, 67, 1867
350		11	13	16:30	N	75	W 40 N	Leonid		3+	C	Proc. Am. Phil. Soc. 10, 357
351		11	13	17:01	N	74	W 43 N	Leonid ?	F	1	Y	Proc. B.M.S. 4, 67, 1868
352		11	13	17:01	N	74	W 43 N	Leonid ?	F	1	Y	Proc. B.M.S. 4, 67, 1868
353		11	13	17:07	N	74	W 43 N	Leonid ?	F	1.1	Y	Proc. B.M.S. 4, 67, 1868
354		11	13	17:41	N	74	W 43 N	Leonid ?	F	1.1	Y	Proc. B.M.S. 4, 67, 1868
355		11	14	-	N ?	4	E 51 N		-	1		Jahr. A. & G. 12, 1901
356		11	14	-	N ?	61	W 16 N		-	Some		Jahr. A. & G. 12, 1901
357		12	31	19:30	T	1	W 51 N	(348 + 33) ?	-4	40	D,S	B.A.A.S. 37, 356-390, 1868; H.C. 517; K 17
358	1868	6	5	23:40	D	97	W 39 N	69 + 24	>M, B	17	L	Am. Jour. Sci. 2,46,429, 1868
359		6	14	10:30	N	8	E 52 N		F	3+	Y	Wochen. 11, 227, 1868
360		7	12	10:15	N	8	E 52 N		-4	2	Y	Wochen. 11, 237, 1868
361		8	10	12:25	N	2	W 53 N	Perseid	-4	0.5	D,S,R,P	B.A.A.S. 37,379, 1868; K 18
362		9	5	8:15	N	8	E 47 N	14 -2	-2	2+	Y	C.R. 69,326, 1869; H.C. 332 b
363		9	8	9:30	N	8	E 52 N		-	2+	M	Wochen. 11, 374, 1868
364		11	13	-	-	13	E 52 N		-	2		Jahr. A. & G. 12, 1901
365a		11	13	11:17	N	75	W 40 N	Leonid	Br	10	S	B.A.A.S. 38,291, 1869)
365b		11	13	11:25	N	74	W 41 N	Leonid ?	-5	8	C,P	Am. Jour. Sci. 2,47,410, Aph.) same Jour. 26, 107, 1907)
366		11	13	11:34	N	75	W 40 N	Leonid	Br	7	S	B.A.A.S. 38,291, 1869
367		11	13	12:20	N	4	W 40 N		X	Sev.	K	A. N. 72,354, 1868
368		11	13	12:25	N	77	W 39 N	Leonid ?	-3	10	Y,E	'Nov. Met. 1868', Eastman
369		11	13	12:30	N	77	W 39 N	Leonid ??	-4	30	R	'Nov. Met. 1868', Eastman
370		11	13	13:16	N	74	W 41 N	Leonid	>-3	44	D,S,P	Am. Jour. Sci. 2,47,121 + 408, 1869; K 12
371		11	13	13:53	N	74	W 41 N	Leonid	Br	0.5 *	S	Am. Jour. Sci. 2,47,410, 1869
372		11	13	14:33	N	4	W 40 N	Leonid	Br	10	R	B.A.A.S. 37,244, 1868; A. N. 72,353, 1868
373		11	13	14:45	N	74	W 41 N	Leonid ?	-5	10	M	Am. Jour. Sci. 2,47,410, 1869
374		11	13	14:46	N	0	52 N	Leonid	-3	1+		Gr. Obs. 1868, 98 No. 4
375a		11	13	14:48	N	74	W 41 N	Leonid ?	Br	3	D,B	Am. Jour. Sci. 2,47,411, 1869)
375b		11	13	15:00	N	76	W 42 N	Leonid	-	Sev.	D	Am. Jour. Sci. 2,47,125, 1869) Possibly same meteor; K 13
376	*	11	13	15:50	N	12	E 42 N	Leonid	F	5	L,D,S	Wochen. 12,335, 1869; Proc. B.M.S. 4, 246, 1868
377		11	13	15:52	N	73	W 43 N	Leonid	Br	3	D	Am. Jour. Sci. 2,47,411, 1869; K 14

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
378	1868	11	13	16:16	N	12 E 42 N	Leonid ?	F	Long		Y	Proc. B.M.S. 4, 247, 1868
379		11	13	16:30	N	75 W 40 N	Leonid	-	Sev.			B.A.A.S. 38, 291, 1869
380		11	13	16:31	N	75 W 40 N	Leonid	-	Sev.			B.A.A.S. 38, 291, 1869
381		11	13	16:51	N	12 E 42 N	Leonid	F	10		C	Wochen. 12, 335, 1869
382		11	13	17:06	N	73 W 41 N	Leonid	Br	6		D	Am. Jour. Sci. 2, 47, 412, 1869; K 15
383		11	13	17:25	N	86 W 39 N	Leonid ?	-	10		D	Am. Jour. Sci. 2, 47, 125, 1869; K 16
384		11	13	17:30	N	71 W 42 N	Leonid	Br	7		D, B, S	Am. Jour. Sci. 2, 47, 413, 1869; K 17
385		11	14	12:20	N	4 W 40 N		X	Sev.			B.A.A.S. 38, 294, 1869
386		11	14	13:30	N	39 W 13 S	Leonid ?	B	15		Z ?	B.A.A.S. 38, 246, 1869
387		12	1	7:14	N	8 E 52 N		-	Long		M	Wochen. 11, 408, 1868
388	1869	5	5	6:32	D	8 E 49 N		-	Long			Met. Mag. 4, 151, 1869; Stone
389		6	7	9:07	T	8 E 52 N	250 + 35	Br	23		D	Wochen. 12, 191 & 198, 1869; H.C. 190; Stone Meteorite?
390		6	17	13:12	N	5 E 43 N		F	18		Y	L'Annee Sci. 14, 15, 1869
391		8	24	7:25	T	78 W 41 N		Br	30		D, R, P	B.A.A.S. 39, 89, 1870; M.W.R. Sept. 1907; K 10d & 11 d
392		9	7	9:50	N	6 E 46 N		Br, B	15 +		Y	Wochen. 12, 328, 1869
393		11	6	6:50	N	4 W 51 N	62 + 37	M, B	50		D, S, P	B.A.A.S. 39, 79, 1870; Nat. 1, 58-267, 1869; K19 MN 309, 1869; Proc. B.M.S. 5, 139, 1870
394		11	13	13:15	N	87 W 30 N		F, B	50		D, C	Am. Jour. Sci. II 49, 245, 1870; K18
395		11	13	14:33	N	120 W 34 N	Leonid ?		8.5		D, R	M.N. 30, 67, 1870; Am. Jour. Sci. 2, 49, 245, 1870
396		11	13	15:32	N	32 E 32 N	Leonid	Br, B	3 +		Z	M.N. 30, 31, 1869
397		11	13	15:40	N	32 E 32 N			5 +		D, S	M.W. 30, 31, 1869
398		11	14	14: ?	N	24 E 38 N	Leonid ?	F	15		L	Wochen. 13, 101, 1870
399		12	12	-	-	4 W 56 N		-	Long			Jahr. A. & G. 12, 1901
400	1870	2	26	9:43	N	2 E 49 N		-4, B				Wochen. 13, 128, 1870
401		8	6	10:05	N	5 W 55 N	Sp.		23		D, P	Backhouse letter
402		8	15	9:00	N	5 W 55 N	312 - 12	F, B	20		D, P	Backhouse letter; Nat. 2, 357, 1870; H.C. 296; K 12 d
403		9	27	6:08	T	10 E 54 N	152 + 47	B	20		S, L	A.N. 77, 321, 1871; H.C. 370; meteorite ?
404		11	3	15:	N	78 E 27 N		F	5		B, E, S	B.A.A.S. 40, 32, 1871, Nat. 3, 209, 1871
405		11	13	10:06	N	5 E 46 N		Br, B	4 +		Z ?	C.R. 73, 154, 1871
406		11	14	-	-	12 E 52 N		-	10			Jahr. A. & G. 12, 1901
407		12	12	5:30	T	14 E 36 N	106 + 32	Br	35		D, E	B.A.A.S. 43, 296, 1874; Denning
408	1871	2	13	9:04	N	3 W 51 N	118 - 3	M, B	10		P, C	B.A.A.S. 40, 32, 1871; H.C. 57; Bruun 47, 41, 1908
409		2	27	10:58	N	2 E 49 N		-	60 +			Wochen. 14, 239, 1871
410		3	17	10:49	N	0 46 N	345 + 50	B	60		Z ? , S, E	C.R. 72, 328 + 383 + 1871; H.C. 97
411		4	22	10:37	N	9 E 45 N	231 - 7	- 3	3.5			B.A.A.S. 40, 36, 1871; H.C. 137
412		4	30	14:30	N	79 W 9 N		Br	2		Y	Nat. 4, 149, 1871
413		7	13	10:06	N	3 E 46 N		Br, B	5 -		Y	C.R. 73, 154, 1871
414		8	10	12:31	N	1 W 52 N	Perseld		30		S	B.A.A.S. 41, 83, 1871; 43, 278 + 284; 1874; Denning
415		9	6	19:07	T	10 E 45 N		-5, B	2		Y	Pub. Brera 7, 17
416		9	8	11:13	N	30 E 31 N		Br, B	3.3		C	Am. Jour. Sci. III 2, 474, 1873
417		9	14	7:32	N	18 E 48 N		F	2			Wochen. 14, 411, 1871
418		11	14	16:00	N	7 E 45 N	Sp. ?	- 3	4		S	Pub. Brera 7, 103
419		12	6	8:15	N	1 W 53 N	Sp.	-4, B	3		Y	B.A.A.S. 41, 113, 1872; H.C. 485
420		12	8	11:44	N	11 E 44 N	Sp.	> 1: B	8			Pub. Brera 7, 108 (No. 8938)
421		-	22	8:15	N	99 W 20 N		B	10		Y	Am. Jour. Sci. III 3, 235, 1872
422	1872	5	15	14:45	N	100 W 15 N		Br, B	15 -		K, R	B.A.A.S. 43, 368, 1873
423		8	9	9:53	N	13 E 44 N	Perseld	M	2			Pub. Brera 7, 53 (No. 4346)
424		8	11	10:10	N	13 E 44 N			60		Z ? , K	Pub. Brera 7, 69
425		8	30	17:15	T	12 E 42 N	90 - 14 ?	Br	15		S	B.A.A.S. 44, 250, 1875; Wochen. 15, 299, 1872; stones
426		10	24	-	-	34 E 47 N		-	Long			Jahr. A. & G. 12, 1901
427		11	27	6:	T	22 E 39 N	Biellid ?	Br	8 +		Y	Met. Mag. 7, 2, 1872
428		11	27	6:35	N	9 E 45 N	Biellid ?	-	21		L, C	B.A.A.S. 42, 390, 1873
429		11	27	7:30	N	2 E 44 N		B	15			C. R. 75, 1553, 1872
430		11	27	7:55	N	1 W 53 N	Biellid	+ 2	2			Am. Jour. Sci. III 5, 152, 1873
431		11	27			8 E 52 N			10			Jahr. A. & G. 12, 1901
432		11	27			8 E 52 N			7			Jahr. A. & G. 12, 1901

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	δ	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D										
433		11	27	11:22	N	58 E 20 S		Biellid ?	-	4		M	B.A.A.S. 42,392,1873; Mat. 7,232, 1873
434		11	27	11:44	N	58 E 20 S		Biellid	-	1 +			B.A.A.S. 42,392,1873; Mat. 7,232, 1873
435		12	12	4:53	T	87 W 39 N			Br, B	Sev.		E	Am. Jour. Sci. III, 5,318,1873
436	1873	5	15	8:05	T	53 W 48 N			Br, B	30		K	Am. Jour. Sci. III, 6,154,1873
437		6	17	8:46	T	17 E 50 N		249 - 20		45		S	B.A.A.S. 43,270,1874; H.C. 200
438		6	-	4:30	D	12 E 54 N				270		M, P	Sirius 34; 29,56,1901; K 13
439		9	20	10:57	N	3 E 46 N			Br, B	10		D	C.R. 77,678,1873
440		9	22	17:10	T	72 E 30 N		320 + 20	> - 1	45		M, S	B.A.A.S. 44,237,1875; Farrington; A.R. 12, 69, 1874; stones
441		10	13	9:41	N	16 E 48 N			X	25 +		Y	A.N. 82,289,1873; B.A.A.S. 43, 345,1874
442	1874	8	10	-	N	18 E 48 N			- 5	2.6			A.N. 84,357,1874; date ?
443		9	1	9:00	N	5 W 50 N			Br	3		Y, P	B.A.A.S. 44,206,1875
444		9	2	10:53	N	1 W 53 N			2/3 M	2		K	B.A.A.S. 46,102,1877
445		10	11	8:55	N	0 53 N			Br	6		Y, P	B.A.A.S. 44,202,1875; Met. Mag. 9, 144,1874; Mat. 10,482,1874
446		10	17	17:10	N	12 E 48 N			X	3		Z, K	Sirius 34,14,1901
447		12	17	10:00	N	2 E 49 N			Br	1 +		Y	Mat. 11,154,1874
448	1875	2	10	6:00	T	2 E 46 N		53 + 50	Br	20		S	C.R. 80,444 + 541 + 575 + 683, 1875; H.C. 49; meteorite
449		8	10	13:24	N	2 W 55 N		Perseid	- 5	4.5		D, L	Backhouse letter
450		9	11	11:00	N	3 W 56 N			Br	3.5		S, R	B.A.A.S. 45,124,1876; Mat. 12,460, 1875
451		10	24	-	-	9 E 55 N			-	45			Jahr. A. & G. 12, 1901
452		12	27	9:20	N	95 W 40 N		355 + 52	B	15		L	B.A.A.S. 44,170,1875; 104 + 150, 1876; H.C. 512
453	1876	6	27	23:27	D	15 E 60 N		180 + 44	B	2		Y	Wochen. 24,270,1881; Mat. 16,238, 1877; meteorite
454		7	8	8:45	N	85 W 42 N		305 + 7	1/2 M, B	40		Y ?	Proc. Am. Phil. Soc. 16,590,1877; H.C. 215, Rep. Signal Off. U.S.A. 1877, P. 287
455		7	17	8:30	T	17 E 48 N		260 + 45	- 4	12		S	Wochen. 19,364,1876; K 14 d; H.C. 226
456		8	10	9:54	N	2 W 52 N		Perseid	- 3	5.5		D	B.A.A.S. 45,132,1876; Denning
457		8	11	11:24	N	0 52 N		Perseid	> - 4	1		Y, S	B.A.A.S. 45,134,1876, A.R. 14, 216, 1876
458		8	12	9:04	N	8 E 52 N		Perseid	F	Many		Y	Wochen. 19,341,1876
459		9	19	10:14	N	2 W 52 N		14 + 6	- 2	3		D	B.A.A.S. 46,108,1877
460		9	24	6:30	T	0 51 N		285 + 35	- 5	16		D, C, P	B.A.A.S. 46,138,1877; H.C. 363
461		10	18	14:00	N	72 W 42 N		Orionid ?	1/2 M	15 +		C	B.A.A.S. 46,110,1877
462		10	22	11:30	N	2 W 53 N		Sp	1/3 M	8 ±		Y	B.A.A.S. 46,110,1877
463		11	17	4:24	N	162 W 64 N			M	82		D, S	Rep. Signal Off. U.S.A. 86, 1877
464		12	11	5:45	T	52 E 14 N			X	12 ±		S	Met. Mag. 11,10,1876
465	1877	3	16	8:	N	26 E 34 S			< M, B	1 -		A	B.A.A.S. 46,118 + 193,1877
466		4	29	8:37	N	20 E 66 N		146 ± 0	S, B	100		D, S, Y	A.N. 89,279,1877; H.C. 144; K20; Wochen. 23,4,1880; 24,301,1881; (meteorite ??)
467		9	11	8:07	N	7 E 47 N			B	11		C	B.A.A.S. 47,280,1878
468		9	28	7:45	N	9 E 55 N			M +	75		D, S, P	B.A.A.S. 47,280,1878; Kohl; K15d
469		10	2	8:58	N	2 W 52 N		227 + 52	> - 4	3		D	B.A.A.S. 47,280,1878; Denning; Mat. 16,550,1877
470		10	19	6:13	T	6 W 53 N		20 + 45	Br	10		D, S, P	B.A.A.S. 47,288,1878; H.C. 400
471		11	20	P.M.	D	79 W 37 N			Br, B	Long			M.W. 38,229,1878
472		11	27	6:	T	75 E 21 N			F, B	6 +		B	Die Naturf. 12,66,1879
473	1878	1	24	7:06	N	96 W 32 N			B	?		D, L	M.W.R. 6,12,1878
474		3	24	22:22	D	3 W 56 N		328 - 15	Br	15		C	B.A.A.S. 47,18 + 32 + 291 + 302, 1878; H.C. 106
475		5	31	14:50	N	83 W 42 N			Br	3 -			M.W.R. 6,11,1878
476		7	5	15:00	N	86 W 40 N			F	1		Y	Rep. Signal Off. U.S.A. 555, 1879
477		7	29	10:20	N	3 W 55 N		306 + 28	< M	1		Y	B.A.A.S. 47,302,1878; H.C. 249
478		8	7	10:53	N	8 E 52 N			- 5	Long		K	Wochen. 21,295,1878
479		8	23	10:50	N	91 W 42 N			Br	?		D, K	M.W.R. 6,13,1874; Sept. 1907; K 19
480		8	24	9:24	N	8 E 52 N			-	Long		Y	Wochen. 21, 297, 1878
481		9	6	9:10	N	9 E 50 N			F	5		Z, K	Wochen. 21, 312, 1878

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
482	1878	9	22	8:45	N	8 E 52 N		Br	Long		B,B	Wochen. 21, 351, 1878
483		11	22	8:	N	121 W 37 N		1/8M B	3			Rep. Signal Off. U.S.A. 616, 1879
484		12	28	-	N	9 E 48 N		I	2 -			Wochen. 22, 8, 1879
485	1879	2	1	-	D	120 E 30 S		M	45			Nat. 20, 121, 1879
486		2	2	10:45	N ?	86 W 40 N		I				Proc. Am. Phil. Soc. 18, 245, 1879,
487		2	20	8:	N	87 W 36 N		Br	1 ?			Rep. Signal Off. U.S.A. 664, 1879
488		3	14	15:53	N	87 W 39 N		B	Sev.		L	Proc. Am. Phil. Soc. 18, 245, 1879
489		9	5	7:10	T	114 W 39 N		Br	45		S	Rep. Signal Off. U.S.A. 621, 1880
490		10	5	5:45	T	1 E 45 N		X	20 +		D,S	C.R. 89, 871, 1879
491		10	16	10:46	N	12 E 51 N	282 + 48	-2	16		C,S	Wochen. 22, 384, 1879; H.C. 396
492	1880	8	6	10:	N	86 W 38 N	Perseid ??	Br	3			M.W.R. 8, 15, 1880
493		8	10	-	-	10 E 56 N		-	3			Jahr. A. & G. 12, 1901
494		9	5	9:30	N	71 W 42 N		Br	1.5		Y	M.W.R. 8, 924, 1880
495		9	21	-	-	112 W 34 N		F,B	4			Rep. Signal Off. U.S.A. 923, 1881
496		12	9	5:15	T	82 W 32 N		Br	20		D,S	M.W.R. 8, 16, 1880
497	1881	10	17	14:20	N	88 W 31 N		B	10		Y?	M.W.R. 9, 23, 1881
498		11	16	6:48	N	87 W 36 N	Sp.	-6	15 *		D,S	Sid. Mes. 1, 174, 1882; K21; Nat. 25, 173, 1881
499		12	8	-	-	3 W 53 N		-	?		L	Jahr. A. & G. 12, 1901
500	1882	5	11	4:	D	107 W 43 N		F	?		Y	Nat. 26, 208, 1882
501		7	9	7:50	T	112 W 34 N			10		D,L,S	M.W.R. 10, -, 1882; K16d
502		8	5	9:	N	87 W 36 N	Perseid ?	0	10 *		D,S	Sid. Mes. 1, 175, 1882; K22
503		8	8	10:00	N	72 W 41 N		B	3			Jahr. A. & G. 12, 1901, M.W.R. Aug. 19, 1882
504		8	11	15:	N	87 W 36 N	Sp.	1 +	1.2 *		D,C	Sid. Mes. 1, 175, 1882; K23
505		8	18	10:30	N	87 W 36 N		I	10 *		D,S,Z	Sid. Mes. 1, 175, 1882; K24
506		8	19	13:30	N	87 W 36 N		I	3 *		D,L,E	Sid. Mes. 1, 175, 1882; K25
507		9	10	7:15	T	97 W 46 N		Br,B	15		Z	M.W.R. 10, IX, 27, 1882
508		10	4	7:40	N	97 W 47 N		Br,B	1		D,S	M.W.R. 10, 21, 1882; K20
509		11	18	13:10	N	37 E 20 N	Leonid ?	Br	20		D	Nat. 27, 149, 1882-3
510	1883	1	3	7:00	N	85 W 42 N		Br	30		Y,R,S	M.W.R. 11, 237, 1883, Jan. 21, 1883; K27
511		5	6	15:10	N	87 W 36 N	Eta Aq.	0	10 *		D,S	Sid. Mes. 2, 148, 1883; K26
512		6	8	7:51	T	58 E 36 N		>M	43		D,S,P	Obs. 6, 271, 1883
513		8	12	9:	N	11 E 59 N		F	1		A	Nat. 28, 425, 1883
514		8	12	-	-	81 W 32 N		-	10			Jahr. A. & G. 12, 1901
515		8	26	11:50	N	4 W 55 N			1		A	Nat. 28, 589, 1883
516		10	30	12:15	N	84 W 35 N		Br	5		Y	M.W.R. 11, 237, 1883
517		12	23		N	96 W 39 N		F,B	13		B	M.W.R. 11, 292, 1883
518	1884	5	27	8:45	T	9 E 63 N		F	5		B	Nat. 30, 200, 1884
519		7	3	8:30	T	77 W 43 N		M, B	10		S,E	Sid. Mes. 3, 167, 1884; Nat. 37, 274, 1888
520		7	12	9:30	N	87 W 36 N		I	4 -		D,S	Sid. Mes. 3, 188, 1884
521		7	31	14:	N	77 W 43 N		Br	Sev. *		D,C	M.W.R. 12, 205, 1884
522		9	5	10:05	N	2 E 49 N		Br	0.5 +		S	C.R. 99, 447, 1884
523		10	23	7:40	N	71 W 42 N		B	1			M.W.R. 12, 263, 1884
524		12	22	11:19	N	8 W 53 N		F,B	17		Y	Nat. 31, 194, 1885
525	1885	7	7	14:	N	77 W 43 N		Br	Sev.		S	Sid. Mes. 4, 178, 1885
526		11	27	6:	N	3 W 56 N		- 5	10		C	Nat. 33, 176, 1885
527		11	27	6:±	N	12 E 48 N		-	1.5		Y	A. N. 113, 138, 1885
528		11	27	6:04	N	2 W 55 N	Bielid	-4	6		D,P	Backhouse letter
529		11	27	6:20	N	14 E 50 N	Bielid	-	1. +		C	A. N. 113, 230, 1885
530		11	27	6:30	N	3 W 56 N	Bielid ?	Br	5		C	Nat. 33, 176, 1885
531		11	27	6:52	N	18 E 60 N	Bielid ?	Br	7		Y	Upsala pub.: A. N. 113, 141, 1885
532		11	27	7:±	N	14 E 36 N	Bielid	-5	2.2		D,S	A. N. 113, 226, 1885
533		11	27	7:±	N	14 E 50 N	Bielid	Br	2 +			A. N. 113, 376, 1886
534		11	27	7:05	N	E N	Bielid	F	7 +		D,B	C. et T. II, 1, 492, 1885
535		11	27	8:±	N	5 W 36 N	Bielid ?	B	25 *		D,R	Nat. 33, 151, 1885
536		11	27	9:	N	102 W 25 N	Bielid???	?	??			Am. Jour. Sci. III 33, 221, 1887 (doubtful train); iron
537		11	27	10:	N	24 E 41 S	Bielid ?	F,B	16		M,K	Ann. der Hyd. 15, 80, 1887; Wochen. 30, 151, 1887
538		11	27	-	N	6 E 51 N	Bielid ?	F	25 ±		Z,L	Wochen. 28, 392, 1885
539		11	27	-	N	60 E 25 N	Bielid	-	8 +			M.W. 46, 122, 1886
540		11	27	-	N	6 E 51 N		B	15			C. et T. II 1, 491, 1885; C.R. 101, 1211

NO.	DATE			HOUR	TYPE	λ ϕ	RADIANT α δ	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D								
541	1885	11	27	-	N	90 E 20 N		<F	15 *		Eng. Mech. 43, 103, 1886
542		12	8	5:48	N	2 W 54 N		F	1		Eng. Mech. 42, 318, 1885
543	1886	8	10	13:34	N	3 W 51 N	Perseid	-4	3.8		Obs. 9, 302, 1886
544		11	2	8:05	N	3 W 51 N	55 + 9 ?	Br	3 -		Obs. 9, 393, 1886
545		12	4	9:17	N	2 W 52 N	162 + 58	-4	1.5		Obs. 10, 66, 1887; H.C. 481
546	1887	3	19	4:	D	145 E 37 S		F, B	30	Z	Obs. 10, 266, 1887; Nat. 36, 93, 1887 gives March 17
547		4	21	9:08	N	34 E 47 N	214 - 13	-5, B	1	D	Wien Ak. 96, 2a, 919, 1887
548		6	12	9:	N	105 W 40 N		B	3		Republican, Denver, Colo., June 13, 1887
549		6	17	7:45	D	2 E 48 N		-8, B	10	Z	Obs. 10, 300, 1887; C.R. 105, 85, 1887
550		8	18	1:	D	57 E 58 N		F	5	Y	Nat. 43, 228, 1891; stones
551		10	18	-	N	122 W 37 N	Orionid	Br	20 *		Sid. Mes. 7, 34, 1888
552		10	19	15:35	N	0 47 N		Br	7 +	M, L	C. R. 105, 963, 1887
553		10	23	4:24	D	15 E 46 N	224 - 8	B	99	D, S, B	Wien Ak. 97, 1 + 665; H.C. 407
554	1888	6	22	12:30	N	81 W 27 N		Br	Long	C, M	M.W.R. 16, 150, 1888
555		7	28	8:02	T	31 E 46 N	227 + 21	Br	10	M, L	Bruun 27, 249, 1888
556		8	13	11:33	N	2 W 52 N	Perseid	-5	3	M	M.N. 49, 19, 1888; Obs. 11, 336, 1888
557		8	19	6:35	D	113 W 46 N		S, B	10		Sci. 12, 132, 1888; M.W.R. 16, 202, 1888
558		10	20	-	N	92 W 31 N			Sev.		Times, Albany, N.Y., 1888 Oct. 26
559		11	13	16:35	N	3 W 48 N	Leonid	7, B	10	S	Cosmos 12, 13, 1889
560		11	13	17:19	N	2 W 52 N	Leonid	F	9	D, P	M.N. 49, 66, 1888; Obs. 11, 427, 1888
561		12	31	7:57	N	4 E 51 N		-5	4 +	Z, L, P	C. et T., 9, 529, 572, 593, 1889
562	1889	2	11	18:52	T	3 W 48 N		Br, B	30	D, S	Cosmos 12, 338, 1889
563		3	22	6:30	T	1 W 52 N		F	45	M	Nat. 39, 537, 1889
564		8	-	15:	N	3 W 56 N		Br	1 +	Y	Nat. 42, 618, 1890
565		11	23	-	-	122 W 38 N		-	Long		Jahr. A. & G. 12, 1901
566		11	23	-	-	151 W 34 S		-	60		Jahr. A. & G. 12, 1901
567	1890	1	17	5:11	T	15 E 47 N	114 + 22	<M, B	30	S	Wien Ak. 99, 11a, 1050, 1890; H.C. 24
568		5	2	5:15	D	94 W 43 N	43 + 36	Br, B	15-	M, S	(Am. Jour. Sci. 39, 521; 40, 318, 1890; H.C. 147; Stones, Sci. 15, 304, 1890)
569		6	8	11:53	N	4 W 50 N		-3	5*	D, P	Backhouse letter, Denning
570		8	6	8:30	N	59 W 43 N		Br	20	C	Ann. der Hyd. 18, 465, 1890
571		8	23	11:30	N	21 E 52 N			20	K	Sirius 24, 34, 1891
572	1891	7	10	11:25	N	3 E 50 N		Br	3 +	E, B, P	C. et T. 12, 312, 1891; BSAF 5, 126, 1891
573		7	29	-	-	11 E 56 N		-	12		Jahr. A. & G. 12, 1901
574		8	9	15:	N	122 W 37 N	Perseid ?	-5, B	1 + *	S	Sid. Mes. 10, 470, 1891
575		8	11	9:45	N	18 E 48 N	Sp. ?	-3	1		O'Gyalla 13-14, 65
576		8	12	10:34	N	18 E 48 N	Perseid	1	1		O'Gyalla 13-14, 67
577		8	26	6:	D	112 W 46 N		B	Sev.		Pittsburgh 'Com. Gazette' 1891 Aug. 24 (pos. 1892)
578		9	8	10:	N	23 W 51 N		Br	4	L, E	Ann. der Hyd. 19, 513, 1891
579		9	27	14:55	N	14 E 48 N			0.9*	D, S, P	M.V.F. 2, 120, 129
580		10	10	9:16	N	9 E 50 N	Sp. ?	-3	10	D, C, P	A.N. 129, 43, 1892; Denning; K 21
581		10	23	8:15	N	1 E 48 N		-	30	K	Sirius 34, 16, 1901
582		10	30	9:13	N	2 W 52 N		>1	10 *	D, S	Obs. 14, 419, 1891; K 22
583		11	14	5:	T	0 45 N		F, B	15	Z	Cosmos. 20, 478, 1891
584		11	15	-	-	74 W 41 N		-	1		Jahr. A. & G. 12, 1901
585		11	18	10:30	N	119 W 35 N		F	40 +	Y	Pub. A.S.P. 4, 37, 1892
586	1892	5	3	16:00	N	44 W 16 N	Eta Aq. ?	Br	3	C	Ann. der Hyd. 20, 293, 1892
587		8	17	8:30	N	N. Atlantic			90		Ann. der Hyd.: Sirius 34, 16, 1901
588		10	18	10:44	N	15 E 48 N	145 + 40	Br	3	Y	Bruun 39, 220, 1900; H.C. 339
589		11	22	8 +	N	25 E 5 S		B	1 +	M	C. et T. 14, 168, 1893
590	1893	3	18	6:07	T	4 W 56 N		Br	45	D, C	J.B.A.A. 3, 335, 1893; Nat. 47, 495 + 516; 1893; 48, 54
591		8	9	-	-	14 E 50 N			10		Sirius 34, 16, 1901
592		8	27	8:40	N	1 E 51 N		Br	6	S	Nat. 48, 425, 1893
593		10	23	-	-	N. Atlantic			35		Jahr. A. & G. 12, 1901
594	1893	11	14	14:50	N	122 W 37 N	Leonid	B	30	D, B	P.A. 1, 192, 1893; X28
595		11	16	15:14	N	5 E 57 N	Leonid	Br	30 +	Y, L	Ann. der Hyd. 22, 35, 1894
596		12	8	-	-	13 E 53 N			1		Jahr. A. & G. 12, 1901
597		12	30	P.M.	N	94 W 42 N		Br	5-		P.A. 1, 281, 1893
598	1894	2	21	7:18	N	3 W 56 N		-3	3	Y	Nat. 49, 419, 1894
599		4	11	15:45	N	3 W 18 S		-	3 +	K, R	Ann. der Hyd. 24, 330, 1896

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
600	1894	7	27	7:30	T	122 W 37 N		225 + 54	F	45	D, C	Lick Obs. Contr. 5, 1895; H.C. 246; Nat. 50, 399, 1894
601		8	9	-	-	14 E 51 N			-	1	Z	Jahr. A. & G. 12, 1901
602		8	10	13:52	N	12 E 42 N		Perseid	-4	2 *	E, L	A.N. 148, 33, 1898; Sirius 27, 105, 1899
603		8	10	-	-	12 E 52 N			-	5		Jahr. A. & G. 12, 1901
604		8	26	10:20	N	3 W 51 N		305 + 79	X, Br	30	D, S, B, P	Mem. B.A.A. 4, 17, 1894; M.N. 55, 238, 1895, etc.; K24; Eng. Mech. 60, 91, 1894
605		10	31	5:13	T	5 E 52 N			M, B	5+	S, B	C. et T. 14, 457; 15, 46, 1893-94
606	1895	1	5	4:35	D	13 E 56 N				3	C, P	Kohl notes
607		4	19	14:47	N	3 W 51 N		Lyrid	-3	5	M, C, E	Mem. B.A.A. 5, 4, +13, 1897
608		10	21	12:05	N	27 E 33 S			F	30	D, E	Mem. B.A.A. 4, 17, 1896
609		11	14	-	-	12 E 51 N			-	41		Jahr. A. & G. 12, 1901
610		11	14	-	-	7 E 51 N			-	10		Jahr. A. & G. 12, 1901
611		11	22	6:50	N	0 51 N				3		Nat. 53, 134, 1895
612		12	12	17:42	N	81 W 41 N		Sp.	Br, B	5	S, B	P.A. 3, 270, 1898
613	1896	1	13	17:45	N	90 W 35 N			?	1	Z ? C	Nat. 53, 612, 1896
614		2	9	21:30	D	4 W 40 N			S+	330	D, R	Nat. 53, 395, 1896; C. et T., 17, 49, 1896; stones
615		2	11	16:45	N	81 W 41 N			-6	10 *	D, C	P.A. 3, 382, 1898
616		3	4	9:14	N	0 53 N			X	16	K	Sirius 34, 16, 1901
617		6	13	10:59	N	0 W 52 N			-4	1-	E	Nat. 54, 221, 1896
618		6	19	8:57	N	145 E 35 S			> M, B	2	Y	Mem. B.A.A. 6, II, 48, 1896
619		9	10	8:45	N	4 W 54 N		72 + 42	-5	0.9*		A.N. 142, 89, 1896; H.C. 339
620		9	24	8:30	N	38 W 34 N			F	7	Y, E	Ann. der Hyd. 25, 219, 1897; K25
621		11	3	6:30	N	112 W 35 N			X	120	C	A.N. 177, 13, 1908; B.S.A.F., 22, 331, 1908
622		11	13	15:40	N	6 W 53 N		Leonid	-1	0.2	D	M.N. 57, 63, 1896
623		11	13	16:31	N	8 E 48 N		Leonid	-3	3	D, B	A.N. 142, 353, 1896; K26
624		11	13	16:33	N	0 53 N		Leonid	-4	2	S	Mem. B.A.A. 6, 2, 51, 1896
625		11	13	17:	N	118 W 34 N		Leonid	-	4+	Y	Pub. A.S.P. 9, 41, 1897
626		11	16	12 +	N	44 E 48 N		Leonid ??	F	Sey.	Y	Nat. 55, 160, 1896
627		12	16	4:30	T	1 E 51 N			Br, B	3-	D, S, P	B.S.A.F. 11, 292, 1897
628	1897	1	2	-	-	18 E 59 N			-	15+		Jahr. A. & G. 12, 1901
629		2	24	3:45	D	110 W 32 N			B	5	Y	M.W.R. 25, 56, 1897; stones
630		2	-	-	-	0 50 N				3	D, S	B.S.A.F. 11, 125, 1897
631		5	5	6:26	D	122 W 38 N			F, B	84	Z	Pub. A.S.P. 9, 146, 1897
632		10	16	-	-	9 E 54 N			-	5		Jahr. A. & G. 12, 1901
633		10	27	17:35	N	79 W 41 N		Sp.	Br	1		P.A. 5, 441, 1897
634		10	-	5:	D	114 W 47 N			F	20	S	Pub. A.S.P. 10, 84, 1898
635	1898	1	2	-	-	9 E 49 N			-	3		Jahr. A. & G. 12, 1901
636		4	25	9:32	N	20 E 45 N			-4	6	D	B.S.A.F. 12, 366, 1898
637		7	5	8:50	N	78 W 43 N			-5, B	6	S, M	P.A. 6, 365, 1898; Nat. 58, 604
638		7	11	7:13	T	88 E 23 N				6	D	Denning
639		8	11	10:20	N	12 E 42 N		Perseid	X	5*	D	A.N. 148, 33, 1898; Sirius 32, 105, 1899
641		9	15	8:45	N	8 E 48 N			Br	2.5		C. et T. 19, 340, 415 + 439
642		10	19	12: +	N	41 W 17 N		Orionid???	Br	10	D	Ann. der Hyd. 27, 520, 1899; K27
643		10	21	10:45	N	12 E 56 N			F	2		Pub. A.S.P. 10, 84, 1898
644		11	7	5:20	T	75 W 41 N		Sp.	F, B	3-	Z	P.A. 6, 566, 1898; B.S.A.F. 13, 137, 1899
645		11	12	11:20	N	71 W 42 N		Leonid	Br	1		P.A. 7, 99, 1899
646		11	12	14:52	N	71 W 42 N		Leonid	Br	1		P.A. 7, 99, 1899
647		11	12	14:57	N	71 W 42 N		Leonid	Br	1		P.A. 7, 98, 1899
648		11	13	12:27	N	73 W 41 N		Leonid???	Br	3		P.A. 6, 85, 1901
649		11	13	13:34	N	73 W 41 N		Leonid???		2		P.A. 6, 85, 1901
650		11	14	13:47	N	122 W 37 N		Leonid	-9, B	42	D, L	P.A. 6, 555, 1898; Pub. A.S.P. 10, 241, 1898
651		11	14	13:50	N	88 W 44 N		Leonid	B	3	Z, E	P.A. 7, 47, 1899
652		11	14	14:57	N	71 W 42 N		Leonid	> -5	2.5	S, P	P.A. 6, 573, 1898; Ladd Obs. notes
653		11	14	15:19	N	12 E 42 N		Leonid	1	15*	D, C, B, I	Sirius 27, 106, 1899
654		11	14	16:13	N	71 W 42 N		Leonid	-4	9-	D, C, B	A.J. 19, 168, 1899
655		11	14	17:17	N	89 W 43 N		Leonid ??	-4	3-	D	Ap. J. 9, 154, 1899
656		11	14	17:20	N	89 W 43 N			-3	1	M, C	Ap. J. 9, 16, 1899

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α δ	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
657		11	15			12 E 42 N				15		Jahr. A. & G. 12, 1901
658		11	16			12 E 42 N				15		Jahr. A. & G. 12, 1901
659		12	21	7:25	N	43 W 23 S			Br	1+		C.R. 128, 190, 1899
660	1899	8	7	13:18	N	105 W 40 N		Sp.	> M, B	Sev.		P.A. 7, 448, 1899
661		8	10	-	N	5 E 50 N			-2	107	A	B.S.A.F. 14, 64, 1900
662		8	12	12:53	N	2 E 49 N		Perseid ?	Br	20	D, E	C.R. 129, 404, 1899; Obs. 22, 379, 1899; K28
663		8	24	9:00	N	11 E 51 N				60	D, C, K	Sirius 32, 250, 1899; 33, 18, 1900
664		9	2	12:05	N	2 W 52 N			> -4	1		Mem. B.A.A. 9, 24, 1901
665		10	10	6:	T	20 E 40 N			B	8-	L	B.S.A.F. 14, 18, 1900
666		10	25	10:08	N	1 W 51 N		Sp.	-5	3	B	Mem. B.A.A. 9, 25, 1901
667		11	14	17:40	N	1 W 52 N		193 + 27	-4	5	D, S	Mem. B.A.A. 9, 19 + 25, 1901; H.C. 453; Nat. 61, 223, 1900
668	1900	1	9	2:57	D	1 E 51 N		280 - 12	F	1	Y	Met. Mag. 35/36, 6, 1900-1, M.W. 72, 426, 1912
669		2	20	18:45	T	0 47 N			B	?	E	B.S.A.F. 14, 149, 1900
670		3	29	9:47	N	122 W 37 N			Br	95	D, K	Publ. A.S.P. 12, 128, 1900
671		4	10	18:45	D	73 W 19 N			Br	45	C	B.S.A.F. 14, 383, 1900
672		4	16	7:05	T	123 W 42 N			F	30	B, Y	Pub. A.S.P. 12, 132, 1900
673		7	15			16 E 51 N				1		Jahr. der Sch. Gesell. Breslau II 37, 1900
674		7	16	8:20	N	98 W 20 N			1/4 M	1		B.S.A.F. 14, 472, 1900
675		7	17	8:47	T	5 E 54 N		249 - 20	Br	47	D	Mem. B.A.A. 10, 1, 19, 1902; H.C. 227; etc.
676		9	2	6:45	D	2 W 55 N		334 + 57	Br	46		Mem. B.A.A. 10, 1, 49, 1902; H.C. 326; Obs. 23, 387, 1900
677		10	27	11:18	N	6 W 52 N		136 + 34	-5	13*	D, P	Nat. 63, 14, 1900; H.C. 415; etc; K29
678		12	7	3:20	D	105 W 39 N		50 + 18	-5, B	60+		P.A. 9, 426, 1901
679		12	16	4:42	T	9 E 56 N			M, B	15+	S, P	Sirius 34, 53, 1901;
680		12	18	12:45	N	2 W 54 N		162 - 5	Br	15	D, C	Mem. B.A.A. 11, 17, 1901; Denning
681		12	25	13:05	N	152 E 33 S			Br	30	D, R	J.B.A.A. 12, 28, 1901
682	1901	1	10	9:03	N	5 E 51 N			-2	10		B.S.A.F. 15, 110, 1901
683		4	29	15:15	N	32 E 48 N		211 + 4	1/4 M	4-		Bruun 41, 160, 1902
684		7	5	8:45	T	0 45 N			Br, B	47	B	B.S.A.F. 15, 419, 1901
685		7	7	10:45	T	6 W 58 N			Br	5	C	Mem. B.A.A. 11, 28, 1903
686		8	11	11:02	N	1 E 51 N			-4	1		Nat. 64, 411, 1901
687		10	19	11:30	N	4 W 51 N		Orionid	-4	5	D, B, E	Mem. B.A.A. 11, 21, 1903; K30
688		10	19	12:03	N	14 E 48 N		Orionid	Br	6*	D, B	Mitt. V.A.P. 11, 109, 1899
689		10	19	16:03	N	14 E 48 N			-3	10*	D, C	Mitt. V.A.P. 11, 109, 1899
690		11	13	6:53	N	3 W 55 N		87 + 34	M	1.5	D, C	Mem. B.A.A. 11, 17, 1903; H.C. 450; etc.
691		11	14	14:	N	110 W 50 N		Leonid	Br	4		P.A. 10, 16, 1902
692		11	14	14:54	N	88 W 40 N		Leonid	Br	16	D, C	P.A. 10, 51+, 107, 1902; Barnard notes; K30
693		11	14	15:05	N	88 W 42 N			X	50±	D, C, P	Barnard letters
694		11	14	15:10	N	93 W 44 N		Leonid	Br	3	Z ?	P.A. 9, 561, 1901
695		11	14	15:15	N	118 W 34 N		Leonid	F	14	D, C	P.A. 10, 16, 1902; M.W.R. Sept 1907; E.M. 74, 381, 1901; K31
696		11	14	16:10	N	110 W 50 N		Leonid	Br	20	D, B	P.A. 10, 51, 1902; M.W.R. Sept. 1907; K32
697		11	14	16:15	N	93 W 44 N		Leonid	Br	6		P.A. 9, 561, 1901
698		11	14	16:50	N	118 W 34 N		Leonid ?	F	6	R	P.A. 10, 18, 1902
699		11	14	17:09	N	71 W 42 N		Leonid	-3	20*	Z?, P, E	P.A. 10, 49, 1902; Denning; K29
700		11	14	17:18	N	93 W 44 N		Leonid	Br	9+	D	P.A. 9, 561, 1901
701		11	14	17:40	N	78 W 38 N		Leonid	< -2	3+	S	Olivier note
702		12	4	5:36	N	0 52 N		263 + 36	> M	5	Z??	M.N. 62, 170, 1901; J.B.A.A. 12, 127, 1902
703	1902	1	24	12:13	N	3 W 54 N			Br	10	Y	Eng. Mech. 75, 32, 1902
704		2	9	7:40	N	0 50 N			-4	1.5		B.S.A.F. 16, 197, 1902
705		7	13	10:50	N	0 51 N		315 + 31	> M	2+	S, Y	Nat. 66, 309, 1902; Obs. 25, 293, 1902
706		8	27	15:13	N	0 51 N			-5	1.5	S	Mem. B.A.A. 12, 1, 29, 1902
707		9	10	12:45	N	17 W 31 N			Br	Sev.	D	Ann. der Hyd. 30, 552, 1902; K32
708		9	15	17:45	T	84 W 42 N			1/4 M	20 ±	S, Y	M.W.R. 32, 172, 231, 1904
709	1903	5	18	9:30	N	12 E 48 N			F	30	S, R, P	Pub. A.S.P. 16, 27, 1903
710		6	28	11:28	N	9 E 49 N			-3	25	D, B	A.N. 163, 251, 1903; K33

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
711	1903	6	30	8:52	T	2 E 47 N			> M	5	D, B	B.S.A.F. 17,381,1903; Obs. 26,331, 1903; Mem.B.A.A. 13,14,1906
712		8	21	13:20	N	0 52 N			M	1		Mem.B.A.A. 13,21,1904-6
713		10	16	10:00	N	4 W 40 N			Br, X	120	D, R, P	B.S.A.F. 18,136,1904; Sirius 37, 6,1904; K34
714		11	1	16:44	N	12 E 49 N		49 - 5	Br	8	Y	Wien Ak. 114,505,1905; H.C. 421
715		11	15	14:00	N	0 52 N		Leonid	-5, B	8*	D	Mem.B.A.A. 13,21,1906; Nat. 69, 65,1903
716		11	15	15:40	N	0 52 N		Leonid	-3	20	D, S, L	Obs. 26,468,1903
717		11	28	10:15	N	158 W 20 N			Br	2+		A.W. 166,381,1904
718	1904	5	18	9:30	N	10 E 56 N			F	30	S	Pub. A.S.P. 17,19,1905
719		8	11	-	N	72 W 44 N		Perseid	Br	4		Nat. 70,536,1904
720		10	12	11:39	N	0 52 N		Sp.	X	30*	S	M.W. 65,89,1904
721		11	14	14:43	N	3 W 51 N		Leonid	-3	3	D, C	Mem.B.A.A. 14,18,1906
722		11	14	14:56	N	88 W 40 N		Leonid	-7	15*	D, R, P	P.A. 13,56,1904; M.W.R. 36,410, 1908
723		11	14	16:24	N	2 W 54 N		Leonid	0	1		Mem.B.A.A. 14,8,1906
724		11	14	17:00	N	10 W 42 N		Leonid	F, B	25	D, S, P	Ann. der Hyd. 33,380 + 476,1905 (2 ships); K35
725		11	16	16:25	N	0 52 N		Leonid	-3, B	1.9		Obs. 28,54,1905; M.W. 65,154,1904
726		12	13	14:45	N	11 E 55 N			F	Sev.	A??	Pub. A.S.P. 17,19,1905
727		12	27	11:14	N	19 E 47 N			F, B	2		Sirius 38,89,1905
728	1905	3	20	0:15	D	11 E 60 N			F, B	15 +	D, S	Kohl Table; Sirius 38,152,1905; K17d
729		6	11	8:43	T	17 E 46 N		218 - 4	jM	60 -	D, C	Bruun 45,161,1906; H.C. 196; etc.
730		7	9	12:27	N	12 E 56 N			F?	4	S	Pub. A.S.P. 18,126,1906
731		8	3	8:56	N	10 E 48 N		317 - 11	M	Long	D	A.W. 170,1,1905; Sirius 38,251, 1905; H.C. 264
732		10	12	11:39	N	0 52 N			X	21*	B, B	J.B.A.A. 15,177,1905; M.W. 65,89, 1904
733		10	13	5:30	T	77 W 41 N			Br	10	M, S, P	Sci. 24,150,1906, reports
734		11	13	7:30	N	8 E 48 N			-	10	S	Sirius 39,19,1906
735		11	29	P.M.	D	18 E 34 S			X, B	120±	M, R	Eng. Mechanic 82,493,1906; B.S.A.F. 20,243,1906
736		12	12	5:	T	108 E 41 N			F, B	30	D, S, P	Cosmos 54,366,1906
737		12	30	4:26	T	3 W 55 N		40 + 23	- 8	15*	D, R, P	Jour. B.A.A. 16,162 + 191; Obs. 29, 134,1906; K18d
738	1906	1	1	5:+	N	25 E 43 N			M	2 -		B.S.A.F. 21,123,1907
739		1	27	8:33	N	2 E 53 N		214 + 53	M	10 +	Y ?	J.B.A.A. 16,253,1906; Nat. 73,427, 1906; M.W. 72,426,1912
740		1	28	8:40	N	16 E 48 N			M?	5		Wien Meteor. Zeits. 23,87
741		6	21	12:30	N	20 W 27 N			Br	15		Ann. der Hyd. 35, 235, 1907
742		7	11	10:55	N	12 E 52 N		350 + 8	jM	5		Wien Ak. 118,185,1909; H.C. 217
743		8	1	7:44	T	15 E 48 N		264 + 22	M-	30	D, S	Bruun, 52,1913; H.C. 258; K19d
744		8	11	12:47	N	78 W 38 N		Perseid	-3	0.3	D, P	Olivier notes
745		11	16	13:20	N	0 52 N		Leonid	1/4 M	3	D	M.W. 67,276,1906; Obs. 34,408,1911
746		12	18	6:08	N	10 E 46 N			F	2	S, P	Kohl Table; A.W. 173,367,1907
747	1907	2	10	5:40	T	74 W 43 N			B	15	D, S, P	M.W.R. 35,447,1907; Denning
748		4	20	6:	D	40 E 50 N			M	(2+)	A	B.S.A.F. 21,309,1907
749		7	11	9:55	N	38 E 45 N			M	1	Y	B.S.A.F. 21,412,1907
750		9	10	8:34	N	15 E 48 N		320 + 29	Br	5	Z	Bruun 47,32,1908; H.C. 344; K36
751		10	5	9:55	N	78 W 42 N		57 - 16	jM	5	C, E	M.W.R. 36,142,1908
752	1908	4	12	6:	D	61 W 32 S			B, M	60	Y	M.V.F.A. 18,52,1908; Nat. Rund. 23,336
753		7	31	11:12	N	2 E 48 N		Perseid	Br	20*	D, C, P	B.S.A.F. 22,458,1908; K37; Nat. 78,612,1908; Cosmos 59,447,1908
754		8	3	9:05	N	34 E 50 N		Perseid		2	S	Jahr. der Sch. Gesell. Breslau II 293,1913
755		10	22	12:55	N	9 E 49 N		33 + 16	-5	30*	D, S	A.W. 179,237,1908; J.B.A.A. 19, 152,1908; H.C. 409; K38
756		11	26	0:35	D	176 E 39 S			Br, B	5	M, L	Obs. 32,173,1909; Nat. 80,128, 1909; Stope
757		11	28	15:51	N	12 E 51 N			Br	29	D, S, R	A.W. 180,14; 181, 94, 1909
758		12	12	7:23	N	16 E 48 N				1		M.V.F.A. 4,1909; G.A. 2,16,1909
759	1909	1	2	10:05	N	32 E 30 N		Quadrantid	Br, B	1.6 *	S, P	J.B.A.A. 19,177,1909

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
760		2	22	7:30	M	2 W 50 N		196 + 20	$\frac{1}{2}$ M	120-	D, C, P	(Obs. 32, 132, +172, 1909; C. et T. 30, (120; H.C. 72; K39, Ann. der Hyd. 37, (519, 1909; Eng. Mech. 89, 112, 1909
761		3	14	7:45	T	18 E 34 S			Br	10	Z, S	Nat. 80, 248, 1909
762		4	20	9:59	M	0 50 N		Lyrid	-5	3	D, R, P	B.S.A.F. 23, 351, 1909; Nature 81, 298, etc.
763		5	8	13:30	M	152 E 34 S		246 + 22	M, B	Sev.		J.B.A.A. 20, 33, 1909
764		6	15	16:10	M	105 E 22 N			Br	9		B.S.A.F. 23, 519, 1909
765		7	9	7:55	T	43 W 44 N			Br, B	10	D	Ann. der Hyd. 37, 520, 1909
766		8	11	12:03	M	12 E 45 N			-	1	C	Mem. Spett. Ital. 38, 172, 1909
767		8	12	9:42	M	0 51 N		Perseid	-5	2.5	D, S	B.S.A.F. 23, 519, 1909; Obs. 32, 349, 1909
768		9	1	8:53	M	1 E 37 N			> M	3 *	Z	B.S.A.F. 23, 520, 1909
769		10	22	16:55	M	2 E 49 N			Br, B	5		B.S.A.F. 24, 21, 1910
770		11	28	P.M.	T	91 W 42 N			F, B	?	Y	P.A. 39, 295, 1931
771		12	7	22:30	D	123 W 38 N			Br	Long		M.W.R. 39, 1909, 1911
772		12	8	14:	M	2 E 49 N			Br	Long	C	B.S.A.F. 24, 175, 1910
773	1910	2	17	6:08	T	0 53 N		72 + 43	-5	30	D	Obs. 33, 134, 1910; J.B.A.A. 20, 332, 1910; H.C. 61
774		4	8	7	T	32 E 55 N			Br	?	D, P	Kareev Report
775		6	18	12:30	M	2 W 46 N			Br, B	20	D, B, K	B.S.A.F. 24, 479, 1910
776		8	19	7:10	T	95 W 31 N			Br, B	20	E ?	M.W.R. 38, 1240, 1910
777		8	28	11:29	M	4 W 53 N			Br	4-	D	Obs. 33, 407, 1910; J.B.A.A. 21, 65, 1911
778		9	23	6:31	T	15 E 48 N		224 - 10	< M	15	S	Wien. Ak. 121, 1883, G.A. No. 64; H.C. 359
779		9	25	7:40	M	1 E 49 N			B	1+		B.S.A.F. 24, 481, 1910
780		10	3	8:50	M	27 E 28 S			$\frac{1}{2}$ M	3	D, A	Nat. 84, 439, 1910
781		10	4	10:45	M	12 E 57 N				2.5	M, B	Kohl Table
782		10	16	21:05	D	89 W 32 N			F, B	45-	Y	M.W.R. 39, 16, 1911; Stones
783		10	28	9:45	M	33 E 15 N			F	8	S	B.S.A.F. 25, 139, 1911
784		10	30	11:28	M ?	13 E 56 N			S	6		G.A.d'Anvers. 1, 8, 1911
785		11	16	12:26	M	5 W 55 N		Leonid	$\frac{1}{2}$ M	20	D	Nat. 85, 150, 1910; Obs. 34, 408, 1911, Eng. Mech. 92, 468, 1910
786		11	24	17:50	T	75 E 23 N			Br	20	S, P	B.S.A.F. 27, 28, 1913
787	1911	4	15	5:50	D	41 W 22 S			B	20	S	B.S.A.F. 25, 278, 1911
788		6	8	11:±	M	99 W 43 N			< Br	16+	D, R, S	P.A. 19, 454, 1911
789a		7	27	11:45	M ?	5 E 51 N			F	3 -	K	G.A.d'Anvers. 1, 40, 1911
789b		7	27	12:	M	9 E 48 N			F, B	1+	C	B.S.A.F., 25, 483, 1911 same meteor as 789a ?
790		9	16	8:15	M	89 W 43 N			Br	5	D, R	P.A. 19, 590, 1911
791		10	3	8:30	M	28 E 26 S				4	D	Denning
792		12	7	22:30	D	123 W 38 N			F, B	Long	Y	M.W.R. 39, 1909, 1911
793	1912	4	7	7:08	T	15 E 50 N		45 + 62	Br	5+	S	Bruun 52, -, 1914; H.C. 120
794		4	7	8:42	M	45 W 13 S			-3	5.77	A, S	B.S.A.F. 26, 519, 1912
795		6	2	5:07	D	22 E 30 S		? - 30	Br	60	D, S, E, P	Eng. Mech. 90, 540, 1912; B.S.A.F. 29, 81, 1915; Union Obs. Cir. 1, Denning; B.A.A. 23, 178, 1913
796		6	3	8:55	M	86 W 40 N			Br	5		The News, Indianapolis, June 4, 1912
797		7	19	6:30	D	110 W 35 N			F, B	?	Y, E	Am. Jour. Sci. IV, 34, 437, 1912; stone
798		8	6	0:10	D	29 E 32 S			$\frac{1}{2}$ S, B	5	R	Union Obs. Cir. 1, 4
799		10	23	7:	M	3 E 50 N			B	2-	B, B	B.S.A.F. 26, 519, 536, 1912; Cos. 67, 481
800	1913	1	10	12:26	M	24 E 52 N			F, B	30+	C, S	A.N. 236, 64, 1929
801		2	27	16:40	M	4 W 50 N			Br	2.3		B.A.A. 23, 274, 1913
802		6	14	8:04	D	1 E 52 N		263 + 64	> M	3-	Y	B.A.A. 24, 23, 1913
803		6	14	10:02	T	3 W 50 N		282 - 23	B	1.5	D	B.A.A. 24, 24, 1913
804		7	21	8:05	T	92 W 42 N			-4	10	S	M.R., S.P.A. 5, 48, 1913
805		9	1	10:16	M	0 53 N			Br	1	S	B.A.A. 24, 198, 1913
806		10	7	10:35	M	4 W 52 N			L	0.5	Y	Nat. 92, 206, 1913
807		10	27	9:12	M	11 E 50 N			-3	8*	D, R, P	A.N. 197, 97, 1914; K40
808		10	29	11:25	M	10 E 54 N			Br	8*	D, S, P	H. und E. 26, 334, 1914; K42
809	1914	1	12	5:45	M	107 W 45 N			X	22	D, S, P	H.A. Frise letter; M.W.R. 42, 38, 1914
810		6	14	8:04	D	1 E 52 N		263 + 64	F, B	3		J.B.A.A. 23, 440, 1913
811		6	24	15:10	M	35 W 85 N			Br	30		M.R., S.P.A., 6, 41, 1914

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	δ	MAX. MAGN.	DUR- ATION	MOTION OF TRAIL	REFERENCES
	Y	M	D										
812	1914	8	14	9:34	N	0	53 N	Perseid	> -4	2			Obs. 37, 364, 1914; M.W. 75, 450, 1915
813		10	24	16:06	N	119 W	34 N	Sp	X	5		D, P, C	F.H. Mays letter
814		12	24	15:15	N	11 E	59 N		F, B	15 ±		D, R	Sirius 48, 92, 1915; K41
815	1915	7	8	12:45	N	24 E	51 N		X	5		D, R	Sirius 48, 267, 1915
816		8	12	13:34	N	87 W	37 N	Perseid	-2	1.5			R.C. Lamb report
817		8	13	11:08	N	1 W	52 N	Perseid	-4	0.5			J.B.A.A. 26, 183, 1915; H.C. 568
818		10	5	10:56	N	5 W	50 N	248 + 72	> 1/2 M	18		D, R, P	J.B.A.A. 26, 23, 1915; H.C. 583; B.S.A.F. 30, 70, 1916
819		10	28	9:00	N	74 W	41 N		-3	1			R. Lambert report
820	1916	1	3	4:35	O	83 E	57 N		F	20+		S, P	Photo by Volkov, mss.
821		4	3	3:25	D	9 E	51 N	357 + 80	Br, B	15		D, S, P	Sirius 51, 177, 1918; H.C. 531; K20d; iron
822		4	3	13:28	N	26 E	53 N		Br	22		D, S	Sirius 49, 121, 1916
823		6	28	15:30	T	4 E	44 N		< M, B	30			B.S.A.F. 30, 430, 1916
824		7	26	10:07	N	0	52 N	35 + 51 (Perseid)	-4	3*		Z	J.B.A.A. 27, 39+110, 1916; H.C. 564
825a		8	7	9:40	N	3 E	46 N		B	4		D, S	C.R. 163, 239, 1916) Probably
825b		8	7	9:48	N	1 E	46 N		4*			D, P	B.S.A.F. 30, 430, 1916) same meteor.
826		9	25	10:30	N	2 E	50 N		Br	15			B.S.A.F. 30, 430, 1916
827		10	17	23:47	D	132 E	45 N			35		L	Sirius 52, 52, 1919; iron
828	1917	5	31	9:55	N	95 W	43 N		F, B	1+		Y	P.A. 25, 483, 1917
829		6	29	9:01	N	15 E	51 N	249 - 20	F, B	18		S, B	Sirius 50, 210, 1917; H.C. 552
830		7	18	4:00	D	123 W	38 N		F	17		D, S	Pub. A.S.P. 29, 191, 1917
831		10	1	10:30	N	99 W	31 N		F, B	45		R, C	Univ. of Texas, Bul. 1772, 1917
832		10	17	14:10	N	0	52 N	Orionid	-6	15		D	J.B.A.A. 28, 118, 1918; H.C. 589
833		10	19	12:17	N	0	53 N	Orionid		6			Denning letter
834	1918	2	25	9:	N	140 W	67 N		S, B	5		L	N.Y. Times 1918-7-8 ± Jour. R.A.S.C. 12, 180, 1918
835		4	23	7:20	T	81 W	34 N		F, B	40		D	M.W.R. 46, 357, 1918; P.A. 27, 126, 1919
836		5	25	21:40	D	31 E	26 S		H	30			Union Obs. Cir. 44, 383, 1919, stones?
837	Summer	-	-	-	-	82 W	33 N		F	1.3 *		C, B, B	P.A. 26, 585, 1918
838	1919	4	23	11:12	N	5 E	46 N	Sporadic	M	3*		Z, C, L	B.S.A.F. 33, 259, 1919
839		6	13	7:15	D	76 W	39 N		F, B	60?		D	P.A. 27, 477, 1919
840		10	27	15:18	N	3 W	51 N	99 - 16	-5, B	2		Y	Obs. 42, 415, 1919
841		12	24	15:25	N	8 E	62 N		F, B	15		C	Himels. 46, 161, 1926
842	1920	1	16	4:55	T	0	53 N	132 + 33	Br	15			Obs. 43, 96, 1920; Wat. 104, 544, 1919
843		5	2	15:30	N	10 E	35 N	Eta Aq.	Br	8		S, E	B.S.A.F. 43, 269, 1920
844		6	8	8:45	N	96 W	36 N		F, B	18		D	Reports to A.M.S.
845		6	30	20:39	D	7 E	50 N	139 - 2	F, B	2		Y	Sonneberg Mitt. Nr. 4; H.C. 554, stones
846		7	17	8:06	T	12 E	50 N	144 + 60	F, B	3			Sonneberg Mitt. Nr. 4; H.C. 559
847		8	11	-	N	68 E	42 N		-	7		D, S, P	Mss.
848		9	7	9:35	N	5 E	45 N		> -4	4		S, E	B.S.A.F. 34, 528, 1920
849		11	7	14:49	N	78 W	38 N		X	10.5		D, P, K	Olivier notes
850	1921	4	19	21:00	D	84 W	32 N		F	2		S	Am. Jour. Sci. V, 3, 211, 1922; P.A. 29, 307, 1921; iron
851		4	27	12:42	N	4 E	51 N		X	40		D, E	B.S.A.F. 36, 171, 1922; G.A.d'Anvers 8, 29, 1921; etc.
852	1922	9	22	6:35	T	16 E	44 N		M	2		Y, K	Sirius 56, 116, 1923
853		11	14	13:11	N	9 E	49 N		X	65		D, C, R	A.N. 218, 47, 1923
854		11	14	15:16	N	94 W	42 N	Leonid	-2	2.9			P. Mead report
855		11	14	15:26	N	94 W	42 N	Leonid	-2	1.5			P. Mead report
856		12	28	5 ±	T	74 E	32 N	Quadr.	Br	20-		D, S	Obs. 46, 94, 1923; H.C. 611; M.B.A.A. 24, 80, 1923
857	1923	8	11		N	71 W	43 N	Perseid	1/3 M	0.7		D	P.A. 32, 195, 1924
858		9	7	7:45	N	0	53 N	260 + 4 ?	Br	12		D, R	Obs. 46, 318, 1923; Wat. 112, 454, +520, 1924
859a		9	11	15:30	N	38 W	40 N	347 + 2 ?	-3, B	20+		Y	Obs. 46, 346, 1923; U.S.N. Hy. 0) Same
859b		9	15	15:18	N	38 W	46 N			20			Jour. R.A.S.C. 17, 356, 1923) meteor!
860		10	30	17:50	N	148 E	33 N		B	6		S, P	M.G. Finne letter
861	1924	1	11	6:00	N	79 W	16 N		Br	7			U.S.N. Hy. 0.
862		4	3	15:16	N	66 W	40 N		Br	6		Y, R	U.S.N. Hy. 0.
863		5	18	12:	N	9 E	50 N			2.5			A.N. 222, 287, 1924
864		5	21	5:40	T	26 E	26 S		B	30		D, S, P	Union Obs. Cir. 66, 328, 1925
865		5	22	7:47	T	76 W	39 N		-	5		D, B, B	P.A. 32, 447, 1924
866		6	14	12:	N	9 E	50 N		-	2.5			A.N. 222, 287, 1914
867		6	-	6:30	D	101 W	48 N		Br	60		Z	A. Halverson report

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α δ	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
868	1924	10	30	10:35	N	57 E	10 N		Br	23	S, Y	Marine Obs. 2, 158, 1925
869		11	1	15:53	N	24 W	49 N		Br	Some *	S, M	Marine Obs. 2, 175, 1925
870	1925	1	5	5:27	N	8 W	45 N		B	7		Marine Obs. 2, 7, 1925
871		3	19	10:56	N	46 E	42 N		Br	1.5 *	D, P	Astapowitsch letter
872		5	3	15:24	N	130 W	35 N		-	25 *	Y	U.S.N. Hy. O.
873		6	4	4:05	D	0	53 N	217 + 14	B	7-		Obs. 48, 229, 1925
874		7	9	10:27	N	60 W	50 N		Br	10	D, R, P	Marine Obs. 3, 109, 1926
875		8	20	8:42	N	32 E	49 N	73 + 64	-8, B	18 *	D, L, P	Mirov. A. B. 24, 2, 1929; Mss.
876		9	5	14:20	N	114 W	26 N		B	4		U.S.N. Hy. O.
877		10	15	16:30	N	57 W	25 N		Br	3		U.S.N. Hy. O.
878		10	16	8:08	N	1 E	46 N		X	33 *	D, R, P	B.S.A.F. 40, 38, 1926
879		12	29	5:16	T	77 W	43 N		< M	20	D, C	P.A. 34, 1, 1926 (one of 7(?) trains: see note)
880	1926	2	12	14:20	N	71 W	31 N		-	5	D, S	R.C. Spaulding letter
881		5	15	7:15	T	153 W	23 N		B	25	S, Y, P	U.S.N. Hy. O.
882		6	1	15:35	N	90 W	30 N		Br	15		N.O. "Picayune" 1926 June 3
883		6	20	15:19	N	50 W	23 N			15		Obs. 49, 287, 1926
884		8	8	19:42	N ?	24 E	38 N		B	Sev.	L	B.S.A.F. 41, 437, 1927
885		9	5	9:02	N	34 E	50 N		F	20 *	D, P	Mss.
886		9	15	10:59	N	0	53 N	140 + 37	M	20		Obs. 49, 314, 1926; Nat. 118, 495, 1926
887		9	17	-	N	97 W	33 N		B	1	D ?	J.H. Logan report
888		10	9	10:16	N	0	53 N	262 + 55	- 5	30 +	D, C	Obs. 50, 120, 1927; 49, 344, 1926
889		10	23	18:20	T ?	-	-		Br	1	S	Marine Obs. 4, 191, 1927
890		11	14	14:	N	74 W	19 N	Leonid ??	Br	10	K, E	U.S.N. Hy. O.
891		11	28	18:	N	74 W	40 N		B	5+		C.S. Maddock report
892	1927	3	29	10:10	N	48 E	52 N			60	D, P	Mss.: 5 Russian reports
893		7	11	12:40	N	86 W	20 N		B	4	Y	U.S.N. Hy. O.
894		7	25	7:36	T	118 W	37 N		Br	10	S	Pub. A.S.P. 39, 332, 1927
895		7	30	9:48	N	3 E	47 N	302 - 12	-9	1	B, B	B.S.A.F. 42, 135, 1928
896		9	4	14:13	N	39 W	36 N		-	3.5	S, L	Hy. O. U.S.N.
897		9	25	8:15	N	74 W	41 N		B	3+	D, L	F.C.H. Unger report
898		10	1	11:35	N	0	52 N	91 + 15	Br	3 -		Obs. 51, 49, 1928
899		10	16	11:55	N	65 W	18 N	Orionid		10	C, K	Mss. from U.S.W.B.
900		10	16	14:47	N	42 E	2 S	Orionid	Br	1.2 *	D	Marine Obs. 6, 205, 1929
901		10	21	7:	N	67 W	15 N	Sp.	Br	60		U.S.N. Hy. O.
902		11	1	12:25	N	21 W	52 N			7	Z ?	Marine Obs. 6, 222, 1929
903		11	1	13:30	N	118 W	33 N		B	8 *	Z, S, E	U.S.N. Hy. O.
904		11	2	14:22	N	76 W	19 N		Br	20	Z ?	U.S.N. Hy. O.
905		11	15	15:25	N	110 W	20 N		< Br	8 *		U.S.N. Hy. O.
906		11	27	15:20	N	120 W	5 N		Br	1-	S	Marine Obs. 6, 226, 1929
907		12	2	4:30	T	101 W	46 N		B	5	E	A. Finch report
908		12	14	6:38	N	74 W	41 N	Geminid	-2	3	Y	P.A. 36, 135, 1928
909	1928	1	2	9:30	N	1 W	17 S	Sp.	-4, 8	5-	Y	U.S.N. Hy. O.
910		1	18	14:20	N	168 E	24 S		Br	1.2		U.S.N. Hy. O.
911		2	15	11:33	N	42 W	23 S		Br	3.3		Marine Obs. 6, 35, 1929
912		4	5	14:	N	74 W	19 N		B	1		U.S.N. Hy. O.
913		4	20	16:	N	74 W	27 N		Br	2		U.S.N. Hy. O.
914		4	21	10:40	N	20 W	18 N	Sp.	B	15		Marine Obs. 6, 79, 1929
915		4	21	15:54	N	78 W	26 N	Lyrld		6	D, S, P	Marine Obs. 6, 79, 1929
916		5	7		T	74 W	53 N			120		Letter from F. Watson
917		6	23	4:10	D	98 W	32 N		S, B	60 +	L, E, P	Univ. of Texas Bul. 2901, 1929
918		7	16	14:35	N	151 W	23 N		B	2.5 *		Mss. U.S.W.B.
919		7	26	18:23	D	28 E	25 S	234 - 52	Br	20	C	Obs. 51, 352, 1928; 52, 121, 1929
920		8	8	8:56	N	98 W	32 N	288 + 64	Br	2	D, R, E	P.A. 37, 275, 1929
921		10	1	7:10	N	120 E	10 N		H, B	15		Pub. Manila Obs. 1, 9, 18
922		10	14	13:27	N	65 W	34 N		Br	10		M.S.S. U.S.W.B.
923		10	15	13:09	N	48 W	40 N	Orionid ?	B	1.4	Y	U.S.N. Hy. O.
924		10	16	14:06	N	43 E	14 N	Orionid ??	B	14+	D, C, S, P	Marine Obs. 6, 220, 1929
925		10	16	15:18	N	176 E	42 S		- 2	1.4	D	Trans. W. Z. Inst. 60, 464, 1929
926		10	20	16:19	N	73 W	41 N		B	20	Y	U.S.N. Hy. O.
927		10	21	15:27	N	68 W	43 N	Orionid	B	7	D, S, P	Marine Obs., 6, 220, 1929
928		11	11	14:14	N	39 W	34 N	Sp.	30			U.S.N. Hy. O.
929		11	12	14:47	N	17 W	54 N	Leonid ?	F, B	6		Mss. U.S.W.B.
930		11	13	13:47	N	92 W	23 N	Leonid ?	F, B	10		U.S.N. Hy. O.
931		11	14	14:50	N	88 W	10 N	Leonid ?	Br	8	B	Mss. U.S.W.B.
932		11	14	15:52	N	63 W	75 N	Leonid ??	B, -4	1.2		U.S.N. Hy. O.

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT	MAX. MAGN.	DURATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
933	1928	11	14	16:	N	89 W 43 N	Leonid	$\frac{1}{2}$ M	12		Y	J. Stebbins report
934		11	15	12:22	N	74 W 35 N	Leonid ??	Br	5+	*	S	U.S.N. Hy. O.
935		11	15	12:28	N	73 W 38 N	Sp.	Br	5			U.S.N. Hy. O.
936		11	15	13:18	N	75 W 36 N	Leonid	Br	4	*	C, E	U.S.N. Hy. O.
937		11	15	14:35	N	59 W 8 N			15		D	Mss. U.S.W.B.
938		11	15	15:16	N	108 W 21 N		Br	15		S	Mss. U.S.W.B.
939		11	15	15:18	N	99 W 19 N	Leonid	Br	10			Tacubaya Mss.
940		11	15	15:38	N	36 W 13 S	Leonid	B	30		D, L, L	Mss. U.S.W.B.
941		11	15	15:55	N	37 W 11 S	Leonid ?		25		E, L	Marine Obs. 6,241, 1929
942		11	15	17:18	N	70 W 27 N	Leonid	Br	1-		Y	U.S.N. Hy. O.
943		11	15	17:40	N	15 E 43 N	Leonid	Br	2.8			U.S.N. Hy. O.
944		11	16	13:35	N	174 E 31 N	Leonid ?		20		L	MSS. U.S.W.B.
945		11	16	16:07	N	98 W 32 N	Sp.	> M, B	8		Y	O.E. Monnig reports
946		11	16	16:48	N	0 53 N	Leonid	Br	5			Obs. 52, 123, 1929
947		11	16	17:20	N	5 E 37 N	Leonid ??	B	12			U.S.N. Hy. O.
948		11	19	15:00	N	9 W 52 N		B	?		Y, C	U.S.N. Hy. O.
949		11	20	13:34	N	94 W 14 N	Leonid ?		1			Mss. U.S.W.B.
950		12	9	15:54	N	120 W 34 N	Sp.		5		Y	U.S.N. Hy. O.
951	1929	1	16	13:18	N	74 W 26 N		Br	2		Y	U.S.N. Hy. O.
952		1	19	15:32	N	94 W 14 N		Br	5		Y	U.S.N. Hy. O.
953		2	1	10:51	N	38 E 47 N		Br	3-			Mirov. A.B. 25, 4, 1929
954		4	8	12:20	N	155 W 3 S		- 5	17		C, P	Marine Obs. 7, 84, 1930
955		5	31	13:58	N	119 E 32 N		Br	1			U.S.N. Hy. O.
956		7	2	9:56	N	130 W 24 S		B	26		D	Mss. U.S.W.B.
957		7	25	9:30	T	12 E 53 N		Br	10		D	Das Weltall 28, 175, 1929
958		8	5	13:43	N	57 W 36 N	Perseid??	Br	3			Marine Obs. 7, 175, 1920
959		8	7	12:33	N	30 W 10 N		?	2	*	D, C	U.S.N. Hy. O.
960		8	11	13:00	N	105 W 39 N		Br	5		D, C, P	A.B. Sperry letter
961		8	19	0:45	D	75 W 45 N		Br	30			J. L. Bedford letter: Jour. R.A.S.C. 23, 378, 1929
962		9	11	15:28	N	136 E \pm 36 N			1			The Heavens (Jap.) 10, 121, 1930
963		11	1	16:20	N	120 W 34 N		?	30			O.G. Martin letter
964		11	16	15:30	N	100 W 17 N		Br	5			U.S.N. Hy. O.
965		12	28	11:20	N	37 E 23 N		-4	1.5	*		Marine Obs. 7, 243, 1930
966	1930	2	16	16:08	N	92 W 35 N		B	5			P.A. 38, 387, 1930: stones
967		5	21	10:31	N	97 W 32 N		-1	2	*	D, Y, K	P.A. 38, 442, 1930
968		6	3	8:30	T	97 W 45 N		Br, B	30+		L	E. Gruse letter
969		6	12	8:	T	89 W 37 N		Br	10		D, C, P	Miss M. L. Jones letter
970		6	30	15:15	N	167 E 26 S		M	3		D	U.S.N. Hy. O.
971		7	4	10:05	N	97 W 47 N		$\frac{1}{2}$ M	1.3		Y	P.A. 38, 510, 1930
972		7	5	-	N	5 W 36 N		Br	5		Y	U.S.N. Hy. O.
973		7	5	14:36	N	14 W 33 N		Br	1		D	U.S.N. Hy. O.
974		7	26	9:51	N	55 W 27 N	Delta Aquarid	-5	7			U.S.N. Hy. O.
975		7	28	12:58	N	87 W 26 N	Sp.	Br	1			U.S.N. Hy. O.
976		8	2	12:15	N	76 W 41 N		Br	1			Mrs. E. Grouser letter
977		9	1	15:52	N	54 W 33 N		B	7		R	U.S.N. Hy. O.
978		9	1	16:30	N	48 W 30 N		B	5			U.S.N. Hy. O.
979		10	14	10:30	N	120 W 34 N		-	10		D, C	U.S.N. Hy. O.
980		11	14	13:57	N	2 W 37 N	Leonid	Br	4		C, P	Marine Obs. 8, 229, 1931
981		11	15	14:30	N	6 W 55 N	Leonid ??	F	Sev.			Nat. 126, 969, 1930
982		11	16	12:03	N	36 W 53 N		B	13		L, P, E	Marine Obs. 8, 229, 1931
983		11	16	13:45	N	114 W 26 N	Leonid ??	Br	45		Y	U.S.N. Hy. O.
984		11	16	13:47	N	81 W 24 N	Leonid	?	16		D, C	U.S.N. Hy. O.
985		11	16	14:28	N	75 W 19 N	Leonid	-4	2		Y	U.S.N. Hy. O.
986		11	16	14:30	N	69 W 30 N	Leonid	?	0.7		D	U.S.N. Hy. O.
987		11	16	14:54	N	82 W 24 N	Sp.	?	10		D, R	U.S.N. Hy. O.
988		11	16	15:11	N	84 W 26 N	Leonid	B	1		B	U.S.N. Hy. O.
989		11	16	15:15	N	92 W 42 N	Leonid ?	Br	10			P.A. 38, 623, 1930
990		11	16	15:17	N	39 E 45 N	Leonid	-9	6		D, P, S	V. Fedyskiu report
991		11	16	15:28	N	143 W 28 N	Leonid	Br	6		Y	U.S.N. Hy. O.
992		11	16	15:35	N	85 W 26 N	Leonid ??	B	Long		L	U.S.N. Hy. O.
993		11	16	15:43	N	74 W 23 N	Leonid	B	25		D	U.S.N. Hy. O.
994		11	16	16:08	N	92 W 42 N	Leonid ??	Br	10		D	P.A. 38, 623, 1930
995		11	16	16:32	N	61 W 43 N	Leonid ?	Sev. *			S, P	Marine Obs. 8, 228, 1931
996		11	16	17:23	N	102 W 17 N	Leonid	Br	3		E, S	U.S.N. Hy. O.

NO.	DATE			HOUR	TYPE	λ °	ϕ °	RADIANT α °	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
997		12	14	14:03	N	77 W	22 N		?	10		U.S.N. Hy. O.
998	1931	2	5	8:55	N	86 W	42 N		F, B	1.5	Y	P.A. 39,223,1931
999		3	25	22:45	D	100 W	39 N		B	Some		Newspaper reports
1000		3	29	9:42	N	43 E	53 N		-	30-	C, P	Kondratiev report
1001		4	21	13:14	N	74 W	21 N	Lyr	B	4	C	U.S.N. Hy. O.
1002		5	16	12:21	T	87 E	54 N		Br	15	Y, L, P	Petrov report
1003		6	3	12:30	N	74 W	40 N		$\frac{1}{2}$ M	0.5	D	P.A. 39,605,1931
1004		6	10	8:14	T	77 W	43 N		B	20	Y, S	12 or more A.M.S. reports
1005		7	12	10:	N	123 W	44 N		< Br	5	D	P.A. 39,605,1931
1006		7	18	3:10	D	97 W	33 N		B	15	Z, L	Tex. O.B. No.29,1934
1007		8	4	7:55	T	92 W	43 N		Br	50 *	D, S, P	W.C. Alvarez letter
1008		8	8	11:50	N	62 W	11 N		F, B	12.5	S	Marine Observer 9,151,1932
1009		8	15	9:36	N	46 W	44 N		Br	2 +	B	U.S.N. Hy. O.
1010		9	17	12:22	N	54 E	5 S		Br	15-		Obs. 54,342,1931
1011		9	27	6:21	T	44 E	13 N			9	M, S, P	Marine Obs. 9,182,1932
1012		10	9	12:20	N	74 W	20 N		B	1.2		U.S.N. Hy. O. (2 Ships)
1013		10	18	9:30	N	90 W	43 N	Orionid ?	Br	15	Y	U.S.N. Hy. O.
1014		11	3	10:00	N	4 E	49 N		-	25	D, S	B.S.A.F. 45,512,1931
1015		11	5	11:25	N	11 E	50 N		?	14 *	D, L, P	C. Hoffmeister letter
1016		11	13	14:10	N	11 E	50 N	Leonid	-3	10+ *	D, L, P	C. Hoffmeister letter
1017		11	15	13:18	N	118 W	34 N	Leonid		1.5		A. M. Brayton report
1018		11	15	13:32	N	118 W	34 N	Leonid		2		A. M. Brayton report
1019		11	15	13:57	N	118 W	34 N	Leonid		4.5		A. M. Brayton report
1020		11	15	14:51	N	107 W	17 N	Sp.	?	2.5	Z, S	U.S.N. Hy. O.
1021		11	15	15:05	N	37 W	53 N			5	Z, L	Marine Obs. 9,201,1932
1022		11	15	17:16	N	99 W	33 N	Leonid	-7	22*	D, P	O.E. Monnig report
1023		11	16	12:05	N	118 W	34 N	Leonid		1.5		A. M. Brayton report
1024		11	16	12:05	N	118 W	34 N	Leonid		1.5		A. M. Brayton report
1025		11	16	12:37	N	74 W	27 N	Leonid	2/3 M	20	D	U.S.N. Hy. O.
1026		11	16	13:07	N	152 E	26 N	Leonid	Br	8.2	C, B	U.S.N. Hy. O.
1027		11	16	13:37	N	59 W	25 N	Leonid ?	?	4	D, S	U.S.N. Hy. O.
1028		11	16	13:47	N	118 W	34 N	Leonid		5		A. M. Brayton report
1029		11	16	13:52	N	76 W	43 N	Leonid	Br	6	D, C	C. R. Gregory report
1030		11	16	13:53	N	74 W	42 N	Leonid	-3	5	Y, P	C. P. Olivier report
1031		11	16	14:02	N	118 W	34 N	Leonid	Br	11	R	C. W. Thompson report
1032		11	16	14:10	N	99 W	19 N	Leonid ?	Br	5		J. Gallo letter
1033		11	16	14:14	N	74 W	42 N	Leonid	-2	12*	D, P	C. P. Olivier report
1034		11	16	14:15	N	131 W	48 N	Leonid	Br	9	L	U.S.N. Hy. O.
1035		11	16	14:18	N	128 W	29 N	Sp.	S	7	D	U.S.N. Hy. O.
1036		11	16	14:19	N	37 W	53 N		F, B	14*	M, R	Marine Obs. 9,201,1932
1037		11	16	14:20	N	100 W	16 N	Leonid	Br	3	D, C	U.S.N. Hy. O.
1038		11	16	14:26	N	37 W	16 S	Leonid	Br	3 +		Marine Obs. 9,201,1932
1039		11	16	14:28	N	93 W	14 N	Leonid ??	?	5	S	U.S.N. Hy. O.
1040		11	16	14:45	N	77 W	43 N			1.5		K. Gell report
1041		11	16	14:52	N	95 W	14 N	Sp. ??	?	10	D	U.S.N. Hy. O.
1042		11	16	15:10	N	99 W	19 N	Leonid	Br	15	D	J. Gallo letter
1043		11	16	15:24	N	39 W	55 N	Leonid	B	6	D, C	Marine Obs. 9,201,1932
1044		11	16	15:25	N	63 W	33 N		Br	25	D, S	U.S.N. Hy. O.
1045		11	16	15:27	N	93 W	15 N		?	2	C	U.S.N. Hy. O.
1046		11	16	15:55	N	77 W	43 N	Leonid	Br	3.5		K. Gell report
1047		11	16	16:01	N	74 W	42 N	Leonid	?	10 *	D, L, P	Proc. Am. Phil. Soc. 72,225,1933
1048		11	16	16:02	N	77 W	42 N			12		K. Gell report
1049		11	16	16:12	N	82 W	30 N	Leonid	Br	15	C, P	M.R. Ensign report
1050		11	16	16:15	N	74 W	42 N	Leonid	0	1	Y	C. P. Olivier report
1051		11	16	16:15	N	77 W	42 N			20		K. Gell report
1052		11	16	16:45	N	77 W	42 N			10		K. Gell report
1053		11	16	16:48	N	79 W	36 N			3.5		J.C. Swanson report
1054		11	16	16:53	N	79 W	36 N			4.8		J.C. Swanson report
1055		11	16	16:59	N	74 W	42 N	Leonid	?	1	Y	C. P. Olivier report
1056		11	16	17:06	N	79 W	36 N			3.0		J. C. Swanson report
1057		11	16	17:12	N	131 W	49 N	Leonid ?	B	10	D, R	U.S.N. Hy. O.
1058		11	16	17:22	N	82 W	30 N	Leonid	?	1.5	Y, P	M. R. Ensign report
1059		11	16	17:25	N	82 W	30 N	Leonid	?	1.7	Y, P	M. R. Ensign report
1060		11	16	17:29	N	74 W	42 N	Leonid	0	3	S	C. P. Olivier report
1061		11	16	17:50	N	82 W	30 N	Leonid	?	1.5	Y, P	M. R. Ensign report
1062		11	16	18:	N	86 W	42 N			2		W. J. Persons report

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α δ	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
1063	1931	11	17	14:14	N	148 E 24 N	Leonid	?	5.5+		C	U.S.N. Hy. O.
1064		11	17	14:26	N	37 W 16 S	Leonid	Br	4-			Marine Obs. 9, 201, 1932
1065		11	17	16:26	N	121 E 25 N	Leonid	?	9		M	Kwasan Bul. No. 233
1066		12	1	18:36	T	79 W 37 N	169 + 34	Br	60+		D, S	Proc. Va. Ac. Sci. 31, 1931-2
1067		12	8	14:00	N	80 W 28 N	Sp.	-4	1		S	U.S.N. Hy. O.
1068		12	31	12:02	N	8 E 52 W	51 - 28	-3	Sev.			A.N. 257, 5, 1935; etc.
1069	1932	1	2	14:28	N	118 W 32 N		Br	24		D, C, P	P.V. Stump report: U.S.N. Hy. O. (2 Ships)
1070		2	14	13:51	N	62 W 19 N		B	3		Y	U.S.N. Hy. O.
1071		3	3	-	N?	22 W 56 N		?	10			U.S.N. Hy. O.
1072		4	5	9:14	N	120 W 32 N	245 + 38	Br	37		M	Reports from 3 Ships: U.S.N. Hy. O.
1073		4	6	9:00	N	123 W 32 N		B	2			U.S.N. Hy. O.
1074		5	3	17:12	N	139 E 35 S	Eta Aq.	1	3		D, P	R. C. Shinkfield report
1075		6	4	11:57	N	84 W 41 N		> M	10		D	P.A. 40, 416, 1932, and letter
1076		7	5	11:50	N	20 W 12 N		Br	5			U.S.N. Hy. O.
1077		7	29	7:52	T	75 W 40 N		-3, B	3		L	2 reports
1078		8	10	4:30	D	94 W 38 N	Sp.	F, B	20-		L	P.A. 44, 93, 1936 and reports; stone
1079		8	10	8:22	T	0 52 N	Perseid		0.5		Y	Obs. 56, 35, 1933
1080		8	11	15:10	N	81 W 33 N	Perseid	-4	1.5		M	W. P. Wamer report
1081		9	21	17:25	T	122 W 44 N	42 + 50	1/2 M, B	15		S	P.A. 46, 274, 1938
1082		10	17	14:16	N	83 W 24 N	Sp.	?	3			U.S.N. Hy. O.
1083		11	14	14:45	N	84 W 36 N		?	1			Miss A. Williams report
1084		11	15	13:00	N	72 W 42 N	Leonid	-2	1.3			Annals H.C.O. 82, 151, 1935
1085		11	15	13:01	N	104 W 18 N	Leonid	-5	1			U.S.N. Hy. O.
1086		11	15	13:07	N	76 W 39 N	Leonid	0	0.5		D	Proc. Am. Phil. Soc. 72, 225, 1933
1087		11	15	14:08	N	76 W 39 N	Leonid	-3	9		D, B, P	Proc. Am. Phil. Soc. 72, 225, 1933
1088		11	15	14:35	N	76 W 39 N	Leonid	-4	9		D, B, P	Proc. Am. Phil. Soc. 72, 225, 1933
1089		11	15	16:05	N	72 W 42 N	Leonid	-3	3		C	Annals H.C.O. 82, 151, 1935
1090		11	15	16:05	N	98 W 33 N	Leonid	0	3.7		Y	Texas O.B. No. 16, and report
1091		11	15	16:15	N	79 W 36 N	Leonid	?	1+		Y	J.C. Swanson report
1092		11	15	16:30	N	100 W 31 N		Br	2		Y	Mrs. F. O. Hester report
1093		11	15	18:	N	74 W 42 N	Leonid	B	2		S	J. A. Kingsbury report
1094		11	16	10:23	N	95 W 39 N	Leonid	X	16+		D, E	E. F. Bowman report
1095		11	16	15:24	N	39 W 55 N	Leonid	Br, B	6		C, D	Marine Obs. 9, -, 1932
1096		11	16	-	N	38 W 45 N		F	5			H. F. Ryan report
1097		11	16	17	N	80 W 26 N		F	8			T. H. Bockhoff report
1098		11	16	17	N	92 W 35 N		F	5		Z ?	A. J. Adams report
1099		12	2	14:14	N	75 W 35 N		Br	8		S	U.S.N. Hy. O.
1100		12	7	7:09	N	80 W 27 N	Sp.	?	1			U.S.N. Hy. O.
1101		12	15	8:24	N	99 W 5 S		- 5	5		Y	U.S.N. Hy. O.
1102	1933	1	2	14:15	N	44 W 32 N	Quad. ?	Br	10		D	U.S.N. Hy. O.
1103		3	23	18:05	T	100 W 36 N	342 + 9	Br	90		D, S, P, E	P.A. 43, 291, 1934; Proc. Am. Phil. Soc. 75, 486, 1935; stone
1104		5	1	15:05	N	47 W 37 N		Br	15		R, P	Marine Obs. 11, 50, 1934
1105		5	5	14:34	N	69 E 39 N		Br	13			I. S. Astapowitsch report
1106		5	17	10:16	N	175 E 42 S	154 - 14	B	5		C, Y	J.B.A.A. 45, 74, 1934
1107		7	27	9:	N	41 W 34 N		Br	1.7			Marine Obs. 11, 95, 1934
1108		8	21	8:05	N	84 W 36 N	279 + 65	> M	3.4		D, B	M.W.R. 61, 326, 1933; Flower Obs. Rep. 23
1109		9	21	8:38	N	69 E 39 N		-4	1.8 *		D, C, P	I. S. Astapowitsch report
1110		9	27	13:35	N	64 W 32 N		Br	13		D, C	U.S.N. Hy. O.
1111		10	7	7:17	N	69 E 39 N		-	8.5 *		Z, B, P	I. S. Astapowitsch report
1112		10	9	7:-	N	1 E 46 N	Drac.	Br	3 *		D	B.S.A.F. 47, 509, 1933
1113		10	9	7:35	N	2 E 49 N	Drac.	Br, B	20+ *		S, P	B.S.A.F. 47, 508, 1933
1114		10	9	7:45	N	1 E 48 N	Drac.	Br	15		Y, S, P	B.S.A.F. 47, 578, 1933
1115		10	9	8:29	N	2 E 49 N	Drac.	Br	4+		D, S, P	B.S.A.F. 47, 503, 1933
1116		10	9	13:53	N	69 E 34 N	Drac. ?	0	0.7 *		D, B, P	I. S. Astapowitsch report
1117		10	13	10:48	N	69 E 39 N		Br	4 *		D, R, P	I. S. Astapowitsch report
1118		10	17 ?	10:26	N	69 E 39 N	Orionid	Br	14		D, E, P	I. S. Astapowitsch report
1119		10	19	11:01	N	69 E 39 N	Orionid	-	9 *		D, R, B, P	I. S. Astapowitsch report
1120		11	9	14:55	N	75 W 38 N	Sp.	Br	6			U.S.N. Hy. O.
1121		11	10	17:45	N	80 W 33 N	Sp.	2/3 M	5 +		S	A.W. Beasley, letter
1122		11	12	14:40	N ?	69 E 39 N		-	2		Y, P	I. S. Astapowitsch report
1123		11	16	14:06	N	19 W 52 N		Br	15		M	U.S.N. Hy. O.) not same meteor
1124		11	16	14:21	N	16 W 55 N		- 3	?		S	U.S.N. Hy. O.)

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	δ	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D										
1125	1933	12	5	5:03	M	19 E 54 N		Sp.	> 0	9		D	A.N. 251,223,1934
1126		12	16	11:46	M	86 W 26 N		Sp.	Br	8		L	U.S.N. Hy. O.
1127	1934	5	5	14:47	M	93 W 28 N		Sp.	Br	13		M,C	U.S.N. Hy. O.
1128		5	11	16:26	M	75 E 10 N		Eta Aquarii	Br	3		D,S,P	U.S.N. Hy. O.
1129		6	5	P.M.	M	164 E 79 S			1	0.1*		D	T.C.Poulter report
1130		6	17	18:45	M	164 E 79 S			?	*		D	T.C.Poulter report
1131		6	17	18:48	M	164 E 79 S			1	0.1*		D	T.C.Poulter report
1132		7	5	8:23	T	25 E 48 N			Br	24		S,B	A.N. 253,291,1934
1133a		8	10	12:58	M	30 E 60 N			Br	1?		S	A. Kokhanov report) same
1133b		8	10	15:58	M	30 E 60 N		Perseid	-9	1.5*		S	V. Petrov report) meteor ??
1134		8	11	8:25	M	91 W 38 N			-7	5*		D,C,P	J.W.Simpson report
1135		8	11	9:46	M	70 W 44 N		Perseid	-5	22		D,S,P	R.M. Dole report
1136		8	11	12:16	M	30 E 60 N			Br	5		S	A. Manotskov report
1137		8	11	12:45	M	15 E 49 N		Perseid	-5	6		D,P	P.A. 42,510,1934, B.S.A.F. 49,201 + 289,1935
1138		8	12	12:	M	50 E 70 N		Perseid	-2	3		D,P	N. Guriev report
1139		9	4	12:	M	50 E 70 N			-1	0.4*			N. Guriev report
1140		9	6	7:20	M	100 W 36 N			Br	10			P.A. 42,518,1934
1141		10	3	17:50	T	39 E 5 S			Br	5		D,S	U.S.N. Hy. O.
1142		10	6	10:40	M	118 W 34 N			Br	2+		D,C	U.S.N. Hy. O.
1143		10	8	8:17	M	74 W 20 M			Br	20		C	U.S.N. Hy. O.
1144		10	8	9:04	M	77 W 22 N			B	2.5			U.S.N. Hy. O.
1145		10	11	10:29	M	0 W 54 N		250 + 75	> M	3		D,E,P	Mat. 134,1004,1934
1146		10	13	11:58	M	69 E 39 N		Sp.	-2	5.2*		D,S	I. Astapow tsch report
1147		10	18	14:29	M	148 E 22 N			Br	2.6			U.S.N. Hy. O.
1148		10	29	7:17	M	75 W 40 N			1/3 M	3.2		Y	A. Johnson report
1149		11	5	7:16	M	43 E 13 N			Br	11		R,P	Marine Obs. 12,147,1935
1150		11	11	12:56	M	84 W 25 N			M,B	8		C	U.S.N. Hy. O.
1151		11	16	15:34	M	136 E 35 N		74 + 31	-5	0.8		D,R,P	H. Inouye report (2 observers)
1152		11	16	17:14	M	140 E 35 N		Leonid	-4	2			Kwasan Obs. Bul. 3,298,1935
1153		12	4	13:16	M	27 W 12 N			B	2?			U.S.N. Hy. O.
1154	1935	1	4	13:00	M	38 E \pm 22 N				3		S,P	Marine Obs. 13,99,1936
1155		2	27	6:08	T	78 W 40 M		80 + 46	-5	12+		D,S	M.W.R. 63,158,1935: Flower Obs.
1156		3	24	7:05	T	10 E 55 N			Br	25		D,S,Ph.	A.N. 255,153,1935: Mat. 136, 224,1935
1157		5	20	12:36	M	85 W 21 N			-5,8	8			U.S.N. Hy. O.
1158		5	27	10:20	M	123 W 46 M			Br	> 1*		S	U.S.N. Hy. O.
1159		6	9	7:39	T	97 W 35 N			< M	40		D,S,P	Tex Obs. Bul. No.57 and reports
1160		6	27	14:00	M	69 E 39 N			+ 1	2.2		D,R	N. Guriev report
1161		7	7	-	M	69 E 39 N			-	?		D	N. Guriev report
1162		7	10	11:18	M	75 W 40 N			-6	10-		K,C	5 reports to A.M.S.
1163		7	9	15:05	M	69 E 39 N			+ 2	0.8*		D,P	N. Guriev report
1164		7	11	14:45	M	73 W 41 N			B	1			C.A. Isterholm report
1165		7	22	12:04	M	136 E \pm 36 N			-	3.8		D,P	Kwasan Obs. Bul. 4,311,1936
1166		7	30	13:37	M	69 E 39 N			+ 1	1.3*		D	N. Guriev report
1167		7	31	8:30	T	79 W 44 N			- 4	10		D,S	Jour.R.A.S.Can. 29,329,1935; report
1168		8	5	13:02	M	69 E 39 N			-	0.8*		D,P	N. Guriev
1169		8	18	12:26	M	30 E 60 N			0	0.3		D,E	V.W. Petrov report
1170		9	6	13:56	M	70 W 28 N			- 2	9		M,L	U.S.N. Hy. O.
1171		9	17	19:46	M	119 W 36 N			M,B	1		Y	U.S.N. Hy. O.
1172		9	27	7:32	M	78 W 13 S			- 5	30*		S	U.S.N. Hy. O.
1173		10	3	9:00	M	16 W 25 N			0.8	Sev.		Y	Marine Obs. 13,132,1936
1174		10	20	11:57	M	69 E 39 N			+ 1	2.1*		D,P	N. Guriev report
1175		10	24	7:17	M	3 E 40 N			- 6	20*		D,R	A.N. 257,251,1935
1176		10	27	10:11	M	69 E 39 N			+ 1	9.5*		D,P	N. Guriev report
1177		11	13	5:05	T	12 E 10 S				21		D,S	Marine Obs. 13,132,1936
1178		11	18	14:39	M	75 W 40 N		Leonid	< Br	1.5		D,C,P	R.S. Whitney report
1179		11	28	16:37	M	14 W 39 N			B	4.5		M	U.S.N. Hy. O.
1180		12	16	10:40	M	69 E 39 N			+ 1	1.5*		D,P	N. Guriev report
1181		12	21	10:42	M	81 W 24 N			B	10		D,C,P	U.S.N. Hy. O.
1182	1936	4	21	14:19	M	12 E 44 N		Lyril	-10	2.5*		D,S,P	E. Loreta report: Jour.R.A.S.Can. 30,250,1936
1183		7	21	11:28	M	63 E 36 N			-	51*		D,S,P	N. Guriev report
1184		7	23	12:00	M	13 E 51 N		23 + 30	-14	30+		D,P	A.N.261,345,1936: Die Sterne 16,203,1936

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT	MAX. MAGN.	DURATION	MOTION OF TRAIL	REFERENCES
	Y	M	D									
1185	1936	7	26	10:36	N	63 E 36 N			-	1.1	D,S,P	M. Guriev report
1186		7	28	9:04	N	12 E 44 N	Sp.	- 4	1.7*		D,C,P	Jr. R.A.S. Can. 30,369,1936
1187		8	9	8:50	N	63 E 36 N		-	4.1		D,B,S,P	M. Guriev report
1188		8	10	15:34	N	70 W 14 N	Perseid ?	Br	2		Y	U.S.N. Hy. O.
1189		8	11	12:22	N	99 W 30 N	Perseid	- 4	5		D,B	R.H. Wilson report
1190		8	11	12:02	N	63 E 36 N		-	1.2		D,P	M. Guriev report
1191		8	11	12:53	N	63 E 36 N		-	1.2*		D,P	M. Guriev report
1192		8	11	14:23	N	63 E 36 N		-	2.2			M. Guriev report
1193		8	11	14:59	N	63 E 36 N		-	1.2			M. Guriev report
1194		8	12	9:28	N	63 E 36 N		-	.4			M. Guriev report
1195		8	12	13:15	N	63 E 36 N		-	8.8			M. Guriev report
1196		8	12	12:35	N	87 W 36 N	Perseid	< M	0.7		C,D	L.J. Wilson report
1197		8	13	9:25	N	63 E 36 N		-	0.6			M. Guriev report
1198		8	13	14:36	N	12 E 44 N	Perseid	0	0.8*		D,C,P	Jr. R.A.S. Can. 30,369,1936
1199		8	13	15:37	N	12 E 44 N	Sp.	- 1	1.2*		D,C,P	Jr. R.A.S. Can. 30,369,1936
1200		8	14	10:14	N	63 E 36 N		-	6.3			M. Guriev report
1201		8	17	7:12	T	98 W 34 N		F, B	15+		Y	P.A. 44,568,1936; stones
1202		9	7	7:30	N	63 E 36 N		-	5.6			M. Guriev report
1203		9	11	8:10	N	63 E 36 N		-	7			M. Guriev report
1204		9	13	14:39	N	63 E 36 N		-	3.3			M. Guriev report
1205		9	15	12:21	N	11 E 50 N		-5	8 *		D,C,P	Hoffmeister report
1206		9	16	13:16	N	11 E 50 N		-1	10 *		D,B,P	Hoffmeister report
1207		9	20	12:10	N	10 W 1 S		Br	13+		D	U.S.N. Hy. O.
1208		10	18	5:23	N	69 E 39 N		- 1				M. Guriev report
1209		10	18	14:31	N	70 W 44 N	Orionid	-6,8	2.2		D,B,P	R.M. Dole report
1210		10	19	11:53	N	89 W 43 N	Orionid	B	7			Amat. Astr. 2, 142
1211		10	19	14:17	N	70 W 20 N	Orionid??	Br	4		D,C	U.S.N. Hy. O.
1212		10	21	11:05	N	80 W 30 N	Sp.	< F	10		D	Dearborn report
1213		10	21	11:34	N	21 E 52 N	Orionid ?	-3	7 *		L	Acta Astr. 3,38,1937
1214a		10	21	14:36	N	87 W 26 N	Orionid	Br	11			U.S.N. Hy. O.) same
1214b		10	21	14:49	N	85 W 26 N		Br	5		C,M	Marine Obs. 14,143,1937) meteor?
1215		10	22	11:03	N	12 E 44 N	Orionid	-2	6 *		D,S,P	E. Loreta report
1216		10	22	11:58	N	61 W 24 N	Orionid	Br	30		D,C	U.S.N. Hy. O.
1217		11	16	11:03	N	12 E 44 N	Leonid	-4	5 *		D,C,P	E. Loreta report
1218		11	16	14:44	N	81 W 29 N	Sp.	-2	3.5		D	R.F. Stevens report
1219		11	24	15:40	N	11 E 50 N		-3	15 *		D,C,P	C. Hoffmeister report
1220		12	6	13:59	N	30 E 34 N		Br	11		D,C	U.S.N. Hy. O.
1221		12	22		N	21 E 52 N	171 + 16	Br	0.8			Acta Astr. 3,119,1937
1222	1937	1	19	6:04	T	72 W 21 N		Br, B	20		D,S,P	Marine Obs. 15,10,1938
1223		2	7	14:16	N	46 W 31 N		M	12		M	U.S.N. Hy. O.
1224		3	21	6:52	T	3 W 51 N		?	8		D,P	Jour. B.A.A. 47,255,1937
1225		5	30	15:09	N	66 W 30 N		Br	3			U.S.N. Hy. O.
1226		6	20	8:33	T	98 W 36 N		> V	10-		D,S	S. Burch report
1227		6	21	7:41	T	117 W 33 N		Br	32		D,C,P	O. B. Landau report
1228		6	21	7:50	T	97 W 33 N		> M	20+		D,C	Texas O.B. 2,83,1938
1229		6	23	8:25	T	79 W 44 N		-5, B	30		D,S	A. Davidson report
1230		8	3	12:57	N	11 E 44 N	Perseid	0	1.5*			Jour. R.A.S. Can. , 32,91,1938
1231		8	7	14:31	N	37 E 22 N	Perseid???	Br	5		D,R,P	Marine Obs. 15,90,1938
1232		8	8	10:08	N	30 E 60 N	Perseid	- 8	2.5		Y,E,P	V. N. Petrov report
1233		8	9	10:48	N	11 E 44 N	335 + 67	- 2	0.4 *		Y	Jour. R.A.S. Can. 32,91,1938
1234		8	11	11:30	N	11 E 54 N	Perseid	- 4.5	3 *		Z,S	Die Sterne, 17,237,1937
1235		8	12	12:14	N	122 W 37 N	Perseid	- 3	1 *		D,C,P	L. Arstianian Report
1236		8	13	12:02	N	77 W 43 N	Perseid	-3	1.5		D,S	C.H. Smith report
1237		8	17	11:31	N	90 W 39 N	Sp.	0	20		D	Jour. R.A.S. Can. 31,398,1937
1238		9	11	11:45	N	30 E 60 N		-4.5	0.7		M	V. N. Petrov report
1239		9	26	7:58	N	4 E 51 N		Br	6*		D,C	Astr. Gaz. 24,99-100; 1937
1240		10	4	11:10	N			X, Br	6.5		S	Marine Obs. 15,139,1938
1241		10	30	8:25	N	21 W 49 N		8	5			U.S. W.B. report
1242		10	30	10:06	N	78 W 31 N		Br	15		D	U.S.N. Hy. O. 2522; 1938-1-5
1243		10	31	14:48	N	147 E 32 N		Br	9		D,C	U.S.N. Hy. O.
1244		11	3	7:22	N	58 W 19 N		-3	4		D,S	U.S.N. Hy. O.
1245		11	6	11:42	N	145 E 27 N		-4,8	0.9		S	U.S.N. Hy. O.
1246		11	12	16:40	N	12 E 44 N	Sp.	-10	11 *		D,S,P	E. Loreta report
1247		12	13	15:50	N	93 W 14 N		- 3	4		D,C,P	U.S.N. Hy. O.; M.D. Berg report
1248		12	18	11:17	N	45 W 31 N		?	11		E,S,P	U.S. W.B. report

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α	MAX. MAGN	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
1249	1938	2	7	5:50	T	79 W 36 N			> M	5+	D	A.C. Howell report
1250		2	18	8:13	N	37 E 23 N			B	2	Y	Marine Obs. 16, 11, 1939
1251		3	5	13:54	N	84 W 25 N			B	3-	D, C	U.S.W. Hy. O.
1252		6	1	7:50	T	117 W 49 N		167 + 13	M, B	60+	D, B, B, P	48 reports to A.M.S.
1253		6	24	5:40	D	80 W 41 N			M, B	15-	D	
1254		7	25	10:11	N	12 E 44 N			-3	5*		E. Loreta report
1255		7	28	11:46	N	12 E 44 N		Perseid	0	0.3*	P	E. Loreta report
1256		7	29	12:28	N	118 W 48 N			1/8 M	5	Z, P	B.C. Parmenter report
1257		10	21	13:35	N	12 E 44 N		Sp.	+1	0.5*		Jour. R.A.S. Canada 33, 114, 1939
1258		10	22	13:52	N	104 W 18 N			-5	1.3*	C	U.S.W. Hy. O.
1259		10	26	12:50	N	88 W 16 N			-5	3.5	C	U.S.W. Hy. O.
1260		10	27	7:55	N	81 W 29 N			-4, B	Sev.	Z	D. Faulkner report
1261		11	21	14:12	N	111 W 23 N			Br	1+	S	U.S.W. Hy. O. 2575
1262		11	20	17:42	N	9 E 49 N		160 + 45	-6	25	D, E	A.N. 269, 276-8; 1939
1263		11	24	15:43	N	15 E 43 N			Br	25	D, E	U.S.W. Hy. O.
1264	1939	1	11	14:02	N	79 W 12 N		170 - 19	-5	7	D, P	P.A. 47, 204, 1939
1265		4	16	15:30	N	57 W 12 N			+3, B	4.8	C, E, D	U.S.W. Hy. O.
1266		4	22	9:45	N	74 W 41 N		Sp.	F	7+	D	M. Preis report
1267		4	28	22:20	D	87 W 32 N			X	Sev.	M	P.A. 48, 93, 1940; The Sky June, 1940, p. 6
1268		5	2	7:01	T	96 W 29 N			F	15	S, Y	The Sky Aug. 1939, p. 6: stones
1269		5	15	9:05	N	74 W 41 N			X	10+	D, P	F.W. Smith report
1270	Summer	-	-	-	-	116 W 48 N			F	30	Y	Wm. Tessin report
1271		7	16	10:00	N	11 E 44 N		Perseid ?	-2	2.5	D, C, P	Jour. R.A.S. Canada 33, 388, 1939
1272		7	16	11:23	N	126 E 31 N			Br, B	2	Y	U.S.W. Hy. O.
1273		8	9	16:15	N	81 W 40 N		Perseid??	-	15	S, P	W.A. Dietrich report
1274		8	12	13:30	N	11 E 44 N		Perseid	-3	7.5*	D, P	Jour. R.A.S. Canada 33, 390, 1939
1275		8	12	14:07	N	11 E 44 N		Perseid	+1	0.5*	D, P	Jour. R.A.S. Canada 33, 390, 1939
1276		8	15	9:55	N	11 E 50 N		Perseid	X	17	D, R, P	Die Sterne 19, 242, 1939
1277		8	16	15:50	N	43 W 24 N		Perseid??	-3	3.5	M	U.S.W. Hy. O.
1278		9	11	13:16	N	79 W 28 N			F	??	D	U.S.W. Hy. O.
1279		9	14	9:35	N	90 W 42 N			1/2 M	6	D, P	P.J. Klaas report
1280		9	16	9:29	N	90 W 28 N			B	0.8*	S	U.S.W. Hy. O.
1281		10	6	14:57	N	61 W 18 N			-3	3.5	C, D	U.S.W. Hy. O.
1282		10	8	11:01	N	113 W 37 N			-	2.5	S	E.A. Kincadek report
1283		10	19	14:59	N	85 W 25 N			F, B	20	D	U.S.W. Hy. O.
1284		10	19	16:25	N	85 W 21 N			-	10	D	U.S.W. Hy. O.
1285		10	20	12:22	N	11 E 44 N		Orionid	-5	6*	D, C, P	Jour. R.A.S. Canada 33, 441, 1939
1286		10	20	13:44	N	11 E 44 N		Orionid	0	1*	D, P	Jour. R.A.S. Canada 33, 443, 1939
1287		10	20	16:24	N	11 E 44 N		Orionid	-7	2.3*	D, S, P	Jour. R.A.S. Canada 33, 443, 1939
1288		10	21	16:18	N	79 W 45 N		Orionid	-3	3*	D, P	Jour. R.A.S. Canada 33, 439, 1939
1289		10	22	15:06	N	10 E 43 N		Orionid	-1	1.3*	P	Mme. Corucci report
1290		11	8	10:08	N	11 E 44 N			-2	3.2*	D, C, P	Jour. R.A.S. Canada 33, 443, 1939
1291a		11	16	14:28	N	70 W 44 N		Leonid	M	41	D, P	R.M. Dole report) same
1291b		11	16	14:19	N	79 W 45 N		Leonid	-3+	5.5*	D	Jour. R.A.S. Canada, 33, 439) meteor 1939: 34, 425, 1940
1292		11	16	16:30	N	79 W 45 N		Leonid	-3	9*	D, P	Jour. R.A.S. Canada 33, 439, 1939
1293		11	16	17:04	N	81 W 40 N			X	1+	Z	Wm. A. Dietrich report
1294	1940	3	22	7:22	T	83 W 42 N			Br	15	D, C, P	Mrs. M. Back report
1295		4	2	14:07	N	88 W 22 N			B	5	-	U.S.W. Hy. O.
1296		4	20	15:52	N	81 W 29 N		Sp.	-6	0.3	D, S, P	A.E. Hayes report
1297		8	11	13:03	N	12 E 44 N		Perseid	-2	0.8*	D, P	E. Loreta report
1298		8	12	13:53	N	12 E 44 N		Perseid	0	2.2*	D, P	E. Loreta report
1299		8	12	14:57	N	12 E 44 N		Perseid	-2	2.2*	D, P	E. Loreta report
1300		8	14	15:37	N	12 E 44 N		Perseid	-2	2.3*	D, P	E. Loreta report
1301		9	11	14:56	N	84 W 25 N			F	1+	Y	U.S. W.B. report
1302		10	21	15:17	N	91 W 28 N		Orionid	-	1.5	D, C	U.S.W. Hy. O.
1303	1941	1	9	18:12	N	73 W 38 N			F, B	2	M	U.S.W. Hy. O.
1304	1850	10	3	8:30	N	73 W 42 N			F	60?	A ?	A.A.S. Proc. 6, 191, 1851
1305	1862	9	-	P.M.	?	0 46 N			F, B	Long		L'Espace Celeste
1306	1865	2	10	-	-	78 E 12 N			M, B	5		Astr. Reg. 3, 162, 1865
1307	1868	6	8	9:50	T	1 W 52 N			Br	4	S	Eng. Mech. 7, 351, 1868
1308	1871*	10	18	9:45	N	8 W 48 N			Br	15 -	C	Astr. Reg. 9, 18, 1871
1309	1873	2	3	9:45	N	145 E 38 S			-4	5	D	Eng. Mech. 17, 171, 1873
1310	1882	2	3	3:45	D	23 E 47 N			F, B	Long		Stones, Wien A.K. 89, 11, 283, 1914; H.C. 45;

NO.	DATE			HOUR	TYPE	λ	ϕ	RADIANT α δ	MAX. MAGN.	DUR- ATION	MOTION OF TRAIN	REFERENCES
	Y	M	D									
1311	1892	8	9	10:00	N	2 W 54 N			1/4M, 8	1		Eng. Mech. 55, 600, and 56, 12, 1892
1312	1893	11	4	11:	N	2 W 56 N			M	2	K	Eng. Mech. 58, 263, and 509, 1893
1313	1896	5	6	10:45	N	2 W 53 N			M	1	C	Eng. Mech. 63, 279, 1896
1314	1896	6	3	15:34	N	1 W 53 N			M	2	Y	Eng. Mech. 63, 374, 1896
1315	1899	11	14	16:51	N	2 W 52 N		Leonid	F	3	D, B	Mem. B. A. A. 9, I, 13, 1901
1316		11	15	16:47	N	0 52 N		Leonid	-3	2	Y	Mem. B. A. A. 9, I, 11, 1901
1317	1908	1	4	10:45	N	3 W 51 N			Br	0.5	D	Eng. Mech. 86, 519, 1908
1318		2	7	10:31	N	1 W 54 N			Br, B	2		Eng. Mech. 87, 37, 1908
1319	1909	8	12	9:25	N	1 E 52 N			Br	5		Eng. Mech. 90, 66, 1909
1320	1911	5	03	8:49	N	2 W 54 N			-4, B	1	Y	Eng. Mech. 93, 335, 1911
1321		12	17	5:	D	31 E 32 N			B	Long	C	Nat. 88, 449, 1911-12
1322	1912	3	6	7:36	N	7 W 55 N			F	Sev.	Y	Eng. Mech. 95, 157, 1912
1323	1915	10	29	7:15	N	45 E 13 N			F	10	C	B. S. A. F. 30, 51, 1916
1324	1917	4	29	-	-	10 E 35 N			-	5	Y	B. S. A. F. 31, 246, 1917
1325	1921	9	23	18:47	T	44 E 12 N			F, B	3.6	Y	B. S. A. F. 36, 107, 1922
1326	1928	8	19	10:23	N	19 E 54 N			-2	0.8	D, C	A. N. 241, 197, 1931
1327		11	15	14:	N	82 W 29 N		Leonid	Br	3		P. A. 38, 105, 1929
1328		11	15	14:	N	82 W 29 N		Leonid	Br	5		P. A. 38, 105, 1929
1329	1930	11	16	14:	N	38 W 45 N			Br	5	K, C	Report from H. F. Ryan
1330		11	16	16: +	N	92 W 34 N			Br	5	Y	Report from A. J. Adams
1331		11	16	17:	N	93 W 35 N			Br	1*	E	Report from H. L. Disheroon
1332		11	16	17:00	N	80 W 26 N			Br	8	Y	Report from T. H. Bockhoff
1333	1931	11	16	-	N	111 W 32 N				10		Sci. N. L. Nov. 28, 1931
1334		11	16	-	N	111 W 32 N				7		Sci. N. L. Nov. 28, 1931
1335	1937	6	21	7:44	T	140 E 36 N			-6, B	4	D, C	P. A. 49, 198, 1941
1336	1941	2	17	18:13	N	116 W 28 N			-3	6	D, C, P	U. S. N. Hy. O.

TABLE II

The first column gives the serial number taken from Table I. Hb gives beginning height and He gives end height of meteor itself in kilometers, the unit everywhere employed. V gives its observed geocentric velocity in km/sec. In Columns 4 and 5, H1 gives height of the upper and H2 of the lower end of the train. Column 6 gives the direction of drift in azimuth, starting at South for 0° and going to West. To get bearings one must add 180°. Vt is the velocity of the drifting train in km/hour. Va is the same velocity expressed in degrees/minute. When the drift was recorded as rapid or slow, without further data, the letters R and S are used in this column. When a double designation, as N/S, appears it means that the direction of motion may be *either* to North or to South, the data being ambiguous. Z denotes that the observer reported no drift of train. Unfortunately, for those which lasted a really long time, there is frequently nothing to show whether the observer meant with respect to the stars, in which case there would be a westward drift due to rotation of Earth, or with respect to Earth's surface, in which case drift would be really zero.

I used my best judgment in such cases. The last column gives other data of value as to the train, if available.

With regard to the direction of drift, in the older cases I have usually taken the results of former computers, but often checked them. In some cases I got different results which are entered here, the others being omitted. I am myself responsible for the reduction of all reports to the A. M. S. and those that came from ships, unless the observer himself specifically recorded the direction of drift. Even then, when possible, I checked. This is also true as to Loreta's work and the manuscript reports from the U. S. S. R., both of which are so numerous. I derived all drifts by plotting on a large celestial globe and passing a great circle through the observed points or at observed angle to the meteor's plotted path. Where this circle cuts the horizon was taken as the direction of drift. Hence a drift of 90° means *towards* the West point, not from it. In the 'Remarks' A stands for N. America, S for the oceans, Q for Southern Hemisphere, E for the land-mass of Europe-Asia and a few in N. Africa.

NO.	M E T E O R			T R A I N					R E M A R K S	
	Hb	He	V	H ₁	H ₂	d	Vt	Va		
22	Km	Km	Km/Sec	Km	Km	°	Km/Hr	°/Min		
24	118	111	8		48	Z?			Height brightest part of train	E
28					111				K1: expanded	E
29						135 ±				E
30						180			Upper part	E
						(270			Remainder	E
33	190	46		60	46	N/S			Train 52 km long; 14 strata	E
43						315				E
45		24		93	24	180			Many parallel currents, dif. vel.	A
55						125			Upper part	E
						Z			Lower part	
56						Z?				E
57	(135	88	48			0			von Niessl's values	E
	78	59	30						Gilbert's values	
59	126									E
63						0?			Smoke: stone meteorite	E
68						270				E
73						cZ				E
75	66	47	64	<66	47>	{ 45			Two parts moving in opposite directions;	A
						{ 225			no data on which is which	

NO.	M E T E O R			T R A I N					R E M A R K S	
	H _b	H _e	V	H ₁	H ₂	d	V _t	V _a		
	Km	Km	Km/Sec	Km	Km	o	Km/Hr	o/Min		
77						180				E
83						45				E
87		100							3 levels	E
93						235		S	Explosion point	A
95						225		S	Small vertical comp.	A
96						NE/SW			Upper part only	A
97						270				A
98						270				A
102	89 +	48				270	300 +			A
115						90		0.7		A
116						Z ±		S	Small deformation	A
127						c 112	151	0.5 +	For 88 km height assumed	A
128						c 112			Slow	E
129						c 135 +				E
134						c 270		0.1	Middle part	S
136						E/W			Contradictory evidence	E
138						c 135		0.2	K2	E
147						Z				E
152						Z			Bent, after 15 min. Z	E
155						45			Z for 7 min., then S W	E
157						Z				A
163	145	92	89					S	Parallel strata; v. low vel.	E
170						Z			Sparks dropped perpendicularly.	E
171	140	16							Particles fell to 16 km; burst at 32 km	E
175						c 11	200	1.2	For 88 km height (assumed?); length train 19 km	A
184						Z +				E
191	96	37	24					S	Certainly small if any	E
194						c 270		0.7		E
196						c 180				E
198						c 202		0.7	For 87 km height; train 24 km long	E
200						Z			Upper part	E
201	219	114				90			Lower part	E
202	56	13				c 315			Upward component	E
205						Z				A
215						270			Middle to E ±, rest E/W	E
216						c 270	129 ?	0.4	On assumptions	E
225	300	16	>58		16	c 270			Large drift	E
228						270				A
229						90			Upper level; first had vertical component	E
230	88	(16)				180			"Parts of train"; rapid drift	E
232	229	104	94			c 0	579	3.4	Burst at 16 km	Q
235	312	104	86						von Niessl's values; Denning's vel. for train; Herchel's values	E
237						112			Or opposite; somewhat ambiguous	E
243						Z				E
245	160	54	67			145				Q
247						W/E			Ambiguous	E
248	39	37	24	(38)	(38)	55			Upper fourth	E
252	56	47				180			Several strata	E
253										E
254	56	40				315			At least 3 strata	E
256									Train in Teles. 24 sec. duration only	E
260						335			Or Z, for middle part	E
263						90				E
264						c Z				E
265	212	59	88			90				E
266	259	12	30			c 63			Train 1/7 total length of path	E
274						Z			Probably middle part	E
275	282	23	30	37	23	Z +				E
279	43	37	50	(40)	(40)				Train 44 x 2.5 km	E
284						0				E
285	170	48	109							E
286	185	45	39						Middle of train lasted longest	E

NO.	M E T E O R			T R A I N					R E M A R K S	
	H _b	H _e	V	H ₁	H ₂	d	V _t	V _a		
	Km	Km	Km/Sec	Km	Km	o NW/SE	Km/Hr	o/Min		
554										A
556	126	76		95	76				Train 29 Km long	E
560	105	60		92	72	c 315	290		Train 24 Km long	E
561						Z			Expansion only	E
562						270				E
567	157	40	54	77	39					E
569						c 315	290	1.0	Height assumed ?	E
579						c 23			Different velocities indicated	E
						(Z				
580						(158	48	0.5	Middle part;	E
						(Z				
582						c 202	463	3.4		E
583						Z				E
588	257	43	81	133	59				At point of appearance	E
590				(93)		c 248	201		Train 634 Km long	E
594						315		0.2	Mean height given ±	E
600					(45)	c 67	105	0.6	Exp. pt. 45 Km	A
601						Z ±				E
604	145	48		93	48	c 315	196	0.7	12 Km long at first; at end oval of 6 Km diam.	E
605						315				E
608						(0			Upper part	Q
						(180			Lower part	
612						90		S	Small, or Z	A
613						Z +			Vertical component at bottom	A
614						c 225		0.2	70° drift	E
615						225			Whole train	A
619	132	105	50							E
621						N/S			10° train, not less than 80 or 100 Km; 5 strata	A
622						225				E
623						135			K 26	E
627						270			Varying velocities	E
630						270				E
636						135				E
638						c 180				E
639						(112			Upper part; K 23	E
						(292			Lower part	
642						135				S
644						Z				A
650						c 23	171	0.3	Height 88-97 Km assumed	A
651						Z			Or slowly to W	A
653						(90			Upper part	E
						(270			Lower part	
654						165				A
655						180		S		A
662						c 45		0.7		E
663						c 45				E
667	114	68	33	114	68	180		0.1	Duration longest lower end	E
670						90				A
675	93	24				c 90			Path length 280 Km	E
676	136	32 ±			40 +	c 225			Path length 134 Km	E
677	122	108	64	119	108	c 315	187	1	K 29	E
678	40	11	42	(25)					Mean height train given, burst 19 Km	A
680						c 270				E
681						90 +				Q
683	102	34	37						Train 0.8 Km wide; path length 147 Km	E
686	153	90								E
687						0		S		E
690	144	83	53			c 45			Path length 264 Km	E
692						225		0.3		E
693						c 90		0.4		A
694						Z +		S	Or to W, v. slow	A
695						169			K 31	A

NO.	M E T E O R			T R A I N					R E M A R K S	
	H _b	H _e	V	H ₁	H ₂	d	V _t	V _a		
	Km	Km	Km/Sec	Km	Km	o	Km/Hr	o/Min		
696						180			K 32	A
699	145 ±	84		137 ±	74	225	18	0.1	K-29; diffusion rate 5.8 Km/h	A
700						135				A
702	146	80	34	115	88				Path length 102 Km, train 42 Km	E
705	144	82				Z +				E
707						202			K 32	E
708						Z ±			Serpentine	A
710				(103)		c 0	400	0.4	Mid-point of train given	E
711						270				E
713						(c 23	64		K 34 Top) vel. on h=88 assumed	E
714	155	61	63	124	88	(c 112	183		Bottom) (for mid-pt?)	E
715	145	85				907		S	Train 12-15 Km wide, 104 Km long	E
716						180		0.5	Burst at 123 Km; path 105 Km long	E
721						c 174		2.6		E
722				(87)		c 225	160		Height assumed 87 Km	A
724						225				E
725	142	71	74	(92)					Mid-pt. of train given; path 97 Km long	E
728	88?	18				180			Burst at 44 Km	E
729	160	69	57	91	69	45			Path length 142 Km, train 40 Km	E
731	183	59 ±	48						Path length 413 Km	E
732						Z?			Or to W slowly	E
733						N/S			4 strata, alternate directions	A
736						(0			Top; several strata	A
						(N/S			Remainder	
737	108	43	24			270		6.7	K 18; path length 116 Km	E
739	95	72	39						Path length 72 Km	E
742	189	100	87	127	104				0.6 Km wide; 90 Km long	E
743	268	74	33	101	74	90			0.5 Km wide; 31 Km long	E
744						158			Lower part	A
745						c 90				E
747						180		S		A
750	255	52	41	158	52	c Z			K 36, 0.1 Km wide; 119 Km long	E
751	104 ±	35 ±							Path 615 ± Km long	A
753						c 292	a 250	1.0	K 37; assuming h=93 Km	E
755	117	76		103	76	(c 225	193	0.3	Upper part; train 35 Km long, K 38	E
						(c 338		0.3	Lower part	
757						NE/SW			3 strata; middle prob. to N.E.	E
760	90	80	35	90	80	c 135	160		K 39; path 250 Km long	E
761						Z ±		S	Parallel strata	Q
762	138	90		121	90	(Z			Top	E
						(c 67	217	1.5	Middle part was 10 Km long	
						(Z			Bottom	
763	102	<13							Explosion point 13 Km	*
767	140	85	57	97	90	c 315	174	-1.0		Q
768						Z				E
773	142 ±	74	24			c 270			Path length 72 Km	E
774						270			Near bottom; rest Z	E
775						45		2. +		E
777						c 90		S		E
778	118	24	44	74	24				Parallel strata; train length 120 Km	E
785	146	72	48	108	88	c 225	169	1.3	Vel. for 92 Km; path length 233 Km	E
786						N/S			5 strata; in S.W. direction drift ??	E
788						338				A
790						E/W			3 strata, middle prob. to W.	A
791						c 0				A
793	93	42	44						Parallel strata; path length 67 Km	A
795				48	24	270				E
802	82	82	41							Q
805	116	108								E
806	119	84		97	84					E
807						225?		S	K 40; possibly only internal motions	E
808						(225			Upper part; K 42	E
						(90			Lower part	E

NO.	M E T E O R			T R A I N					R E M A R K S	
	H _b	H _e	V	H ₁	H ₂	d	V _t	V _a		
	Km	Km	Km/Sec	Km	Km	o	Km/hr	o/Min		
291						180				A
292						180				A
294						180		0.3±	Decreasing vel. in drift, K6	E
295						Z?			Probable interpretation	E
296						90				E
297	58	11								E
298	130	30	42							E
299						225				E
303						315		2.0		E
304						90				E
305					90	?			Vertical component of drift	E
309						c 315	521	2.8	For 97 km height assumed	E
310						c 349	270	2.0	For 80 km height	E
311						c 124	77	0.8	For 97 km height assumed	E
312	160	85		95	85	c 270	180	1.6	Train expanded at rate of 0.16 km/min	E
313						c 0				E
319						c 292				E
321	193	97		105	97	c 180	200		Train expanded at rate of 0.27 km/min	A
322						0				E
323						c 315	274	2.0	For 97 km height assumed	E
325						Z			Or E very slow	E
326				108	98	c 326	338	1.8	Assuming 103 Km alt.	E
328						c 0		1.9		E
334	(115 137)	67 105				90			von Niessl's values, B.A.A.S. values doubtful!	E
341						135				A
342						315		1.8		A
343						315		0.7		A
344						338		0.8		A
345						349			Large drift of 11°	A
346						270		0.6		A
348						180				A
357	148	119	30			270			Slow drift; hopeless disagreement as to results	E
358	126	20							Explosion cloud 2.3 x 1.5 km; Infer Z drift	A
361						315	c 770!	4.0	Very ??; 3 strata	E
362	307	111	88			67	153	0.8	Inclination of orbit 112°	E
370	193	79		95	79	{ 180 0	< 100 100		Height assumed? from Haverford, Pa. Upper part, train 48 km long } from New Lower part } England	A
373				(82)					Mean height	A
375				105	84	180				A
377				(124)		180			Brighter portion of the meteor track; train 16 km long	A
382	137	97				{ 0 180 0		1.0	Drifts as seen from New Haven, Conn; from New York, N.Y. to N by E, 5° in 3 min"	A
383						270			Slow; possibly Z?	A
384					95	180				A
386						Z			Possibly E?; if so slow	Q
389						0				E
391					(64)	c 180	257?		Vel. due to Denning, who gives d to W; mean height	A
393	145	43	55	76	43	c 135	161	0.6		E
394						180		S		A
395						c 292	137	0.9	Height 88-97 Km assumed; 3 strata	A
396						c 90	48	S	Height 88-97 Km assumed	E
397						c 135	193			E
401						0 ±				E
402	74	82		74	82	45			Deflected upwards at 67 Km! where most persistent part of train was; mean height train 74 Km	E

NO.	M E T E O R			T R A I N					R E M A R K S	
	H _b	H _e	V	H ₁	H ₂	d	V _t	V _a		
	Km	Km	Km/Sec	Km	Km	o	Km/Hr	o/Min		
403	166 (83)	16	65	35	16				Train 31 Km long	E
407						c 270	64	0.2	Height 87 Km assumed	E
408	106	32	74	46	44				Train 2° long	E
410	164		> 30			Z			Possibly to W, slow	E
411		69								E
414	145	66		97	77					E
416						180			For center; also vertical component	E
424						Z ±				E
428						90	S		Drift short distance	E
433									Train had vertical component	E
437	163	32	44	64	32				Train 148 x 0.8 Km	Q
438						225 ±			Very uncertain; 9 parallel strata	E
439						45		2		E
446						Z				E
448	192									E
449						c 292	174	0.5	Height 97 Km assumed?	E
452	267	22	26							E
454	142	55								A
455	164	79	29			NW/SE			5 strata	E
456						c 45	319	2.0	Height 105 Km assumed	E
457						c 90	204	1.0	Height assumed?	E
459						c 315				E
460	93	26	24	42	26	c 180		0.9	3 strata	E
463						90		0.3	3 sections	E
466	68	31	34			180		5	Exp. at 35 Km	A
468						c 90			5 strata	E
469						c 180	225	1.9	Height assumed?	E
470						(225	394		Upper part	E
	97	64				(Z	0		Lower part	E
471	113	16								A
473						90				A
474	178	44	59						Von Niessl's values	E
475	80	32	53						Herschel's values	E
479						270				A
481						Z ±				E
489									Several strata	A
490						0		0.5		E
491	122	93	34							E
496						90				A
498						c 225		0.3	Slow	A
501						90			Lower part	A
502						c 0	170	0.5	Assuming average height of ? Km	A
504						c 338	212	0.8	Assuming average height of ? Km	A
505						c 160		0.2		A
506						c 270	373	0.5	Assuming average height of ? Km	A
507						Z			Or N.W.; ambiguous	A
508						23				A
509						90		0.2		A
510						Z			Or to E, very slow	E
511						281		1.7		A
512						225/45			Strata 1,3,5 to N.E.; 2,4,6 to S.W.	E
520						315			Several degrees	E
521						180		S		A
528						c 315 ±				A
531					100	N/S			Mean height	E
532						(45			Upper part	E
						(225			Lower part	E
537						Z ±			Very slow	E
538						180				Q
545	105	45		76	69					E
547	133	3	40			158			Burst at 34 Km	E
548						22				E
553	220	33	48	40	33	c 225	200		Train 21 Km long	A

NO.	M E T E O R			T R A I N					R E M A R K S	
	H _b	H _e	V	H ₁	H ₂	d	V _t	V _a		
	Km	Km	Km/Sec	Km	Km	°	Km/hr	°/Min		
809						(0 (225?		S S	Top) directions Bottom; slight or ?) very ?? Path length 94 Km	A
810	124	47								E
812	137	87	100							E
813						(c 270 (c 7 (c 170 225 N/S/N		0.2 0.± 1.5	Velocity increases downward K 41 3 strata; middle prob. to S Path length 77 Km Path length 68 Km Top; Path length 81 Km Middle Bottom 3 ± strata Path length 146 Km	A
814										E
815										E
817	127	86	64							E
818	132	89	56	103	89	146	150			E
821	156	16	16	70 +	16	(30 (7 (270 NE/SW 7 292		S		E
822										E
824	138	79	60							E
825								1.0		E
829	89	18	36	(73)					Mean height ??; path length 229 Km Path length 210 Km ±	E
831	185 ±	10	60					S	Upper part; path length 56 Km Lower part 88 Km mean height assumed Exploded at 95 Km Lower part moved faster, 12x7 Km at disap.	A
832	116	76	113	108	84	(c 304 (c 304 45 270	129 264 209 250			E
833				(88)						E
835		(95)								E
838						7				E
842	84	71	24						Length of path 72 Km	E
844						135				E
845		29							Train 19 Km long	E
846		23								E
847						23 ±				E
849						c 180				E
851						c 45		1.3		E
853						45				E
856	87 ±	47	40			315				E
858	111	42	32			(0 (180 (0 0? SW/NE 45 90			3 strata; path length 161 Km Direction uncertain 5 strata; burst at 32 Km	E
860										E
864		(32)						S		Q
865										A
871								1.0-		E
873	85	64	34						Path length 98 Km Motion of upper and lower part uncertain V for 90 Km height	S
874						7,225?				E
875	159	78	74	95	78	338	250			E
878						23		1.1		E
879	103	66	21			(270 (90? 90 N/S? (90 (135 (135			V greater; path length 65 Km V less At least 6; very irregular Upper part Central part Lower part Path length 177 Km Very uncertain; ambiguous V great	A
880								4.0		A
881										S
885				118	74					E
886	114	90								E
887						158?				A
888	108	39	32			202				E
892										E
895	118	58	29		>100	c 225	50 <	0.5		E
896						125		3	Knotty train; path length 144 Km One stratum only shown; wide Unaltered for 2 + min.	S
897						90		S		A
898	142	85	61	116	85					E
899						90?			Upper part; rest ???	S
902						7 ±				Q
903						7 ?			Or to W; ambiguous	S

NO.	M E T E O R			T R A I N					R E M A R K S	
	H _b	H _e	V	H ₁	H ₂	d	V _t	V _a		
	Km	Km	Km/Sec	Km	Km	o	Km/hr	m/min		
904						907			Or Z; ambiguous	S
						(225			Top	S
906						(2			Center	
						(45			Bottom	
915						270			Bottom; several others E/W	S
917				27 ±	19 +				Train 24 Km long	A
919	119	53	13						Path length 74 Km	Q
920		75		106	75	c 2			Expansion only, radial V=120 Km/h	A
924						270			Most peculiar curved path!	E
925						270		S	Very slow	Q
927						180			3 variable velocities, lower part of train only	S
937						c 135		2.1		S
940						90				Q
946	145	80	68						Path length 61 Km?	E
953	72	32							Path length 120 Km	E
954						90			3 levels, solution rather ?	Q
956						135		0.1		Q
957		110		110		270?		S	Or Z; 2 observers	E
959						0/Z/0			3 strata	S
960						90			3 strata	A
967		25				c 34			Lower condensation only	A
969						c 135				A
970						250				Q
973						23				S
979						270		S	E at first, then stationary	A
980						270		S	Top and bottom Z; center to E	E
984						350			3 levels for lower part	A
986						E/W			3 strata, vertical component also	S
987						202			Middle; 3 strata	S
990						c 112		2.2	Drift to WNW; then to NW	E
993						225		1 +		S
994						c 270	100	1.0	Height assumed	A
995						90			For strata 2 and 4 out of 5, others Z	S
996						E/W			Upper part; lower Z??	S
1001	113	35	21			20			Upper and lower parts; middle Z,	S
1002						80 ?		S	Very slow or Z	E
1003	92?	92		92?	92	c 0			End part of train drifted S; rest ??	A
1004						Z ±			Zero N-S; small E-W	A
1005						c 23				A
1006						Z				A
1007						345 ±		S	?? and small	A
1014						Z?			Or E very small	E
1015						c 146		0.4		E
1016						c 90		0.5		E
1020						Z +				S
1021						c Z				S
1022						c 292		0.7		S
1025						N/S			2 strata ?	A
1026						270			Lower part; rest ??	S
1027						180			Whole train	S
1029						c 270				S
1031						SSW/NNE			3 strata; some possibly Z	A
1033						c 180		1.0+	Slight change dir. of drift after 2 min.	A
1035						45				S
1036						315			Lower part	S
1037						170			Middle part; rest Z?	S
1041						270			Lower part	S
1042						0 ?			Debris falling only ??	S
1044						c 90		1.0	3 strata	A
1047						c 45		0.7		S
1049						c 338				A
1057						90		2. +		S

NO.	M E T E O R			T R A I N					R E M A R K S	
	H _b	H _e	V	H ₁	H ₂	d	V _t	V _a		
	Km	km	Km/Sec	Km	Km	o	Km/Hr	o/Min		
1066	120	12		43	12	(45 (Z (225	< 15 0 < 15		> 16 Km at 16 Km 12 to 16 Km Path length 1000 ± Km 4 strata Solution an uncertain one ??	A
1068	>150	55	57			-				E
1069						E/W				A
1072	208	115	38	187	115	-				A
1074						c 338		0.7		Q
1075						c 90		0.2		A
1078					20				Train 64 Km long; 1/2 Km wide ±	A
1079	103	68	55	87	68				Length of train 48 Km	E
1081	81	6	28	(81)	6	Z ±		S	Wavy motion only	A
1086		91			91	0				A
1087	119	86		(100)	(106)	15	151		Middle part; vertical component; diam. 1 Km	A
1088	(142)	73		(88)	(100)	67	236		Middle part; vertical component; diam. 3.8x1.3 Km, and horizontal motion	A
1089	(225)	90			100	45 ±			Burst at 91 Km; Visual data	A
1094	(116)	90							Photographic data	
1095						c 180 (45 (Z 180		0.1-	Upper part Where burst	A S
1102								S		S
1103	141	17		102	25	270 ±	280	0.2	Parts of train expanded	A
1105				((96)		296	32		Heights est. ??	E
				((82)	51	67		Train 24 Km long	
1106	62	10	24	50	34	Z			Train 26 Km long, path 84 Km	Q
1108	171	46		108	57	c 270	128 +		Horizontal	A
1109						20		5:		E
1110						315		1.6		E
1111						c Z				E
1112						315		1.7		E
1113						(c Z (c 90		0.2	Upper part; 5 strata indicated, Lower part	E
1114						Z			Or very slow W, 5 strata slightly indicated	E
1115						(c Z (90 75		0.7 9.	Upper part Lower part, 5 strata indicated	E E
1116						180 ±		4.5	Data ambiguous	E
1117						270		0.7	Possibly more ENE; long train, nearly all lasting full time	E
1118									Drift in upper strata twice as fast	E
1119						c 135			Bottom nearly Z, increasing vel. upward	E
1125						45			Or Z	S
1128						90?		S		Q
1129						270				Q
1130						270				Q
1131						270				Q
1133						112				E
1134	76	43	40	72	45	c 220		0.5	Middle, 3 strata; top +bottom Z ±	A
1135						c 353		1.0		A
1137	130	80		100	85	248	200		Assumptions made	A
1138						158		R		E
1139						10		4.		E
1141						225?			Upward ??	E
1142						180		3.0		Q
						(248	210		Height 111 Km; train length 44 Km	E
1145	151	82	34	124	90	(225 (202	260 240		Height 97 Km Height 90 Km	E
1146						90		-1.0	Central part more rapid	E
1149						E/W			3 strata; vertical comp.	S
1151	116	44				45		16.0		E
1152	146	69								E
						(Z		0.0		S
						(0		1.0		
1154						(Z		0.0	5 strata	
						(0		1.0		
						(Z		0.0		

NO.	M E T E O R			T R A I N					R E M A R K S	
	H _b	H _e	V	H ₁	H ₂	d	V _t	V _a		
	Km	Km	Km/Sec	Km	Km	o	Km/hr	o/min		
1155				62	31	(0 (180 (0 (180 (0 (180	121 82 30 52 38 79		Height 62) 47) velocities projected and 44) minimum 42) 39) 29	A
1156	95	80			(72 ±)	90			Mean height; drift considerable	E
1159						180			Central part; top and bottom Z	A
1160						180		2.5		E
1161						180				E
1163						0		1.5		E
1165						c 335		2.5		E
1166						270		5.0		E
1168						260			Central part only	E
1174						(270 (310		4.5	Direction changed	E
1175						c 180		0.5		E
1176						(225 (340		S		E
1177						W/E			About 25 strata, horizontal	Q
1178						c 310		1.3		A
1180						340		0.8		E
1181						0		1.6		S
1182						c 45		0.5		E
1184	129	73	37	(93)		(228 (270	10		Main part; rapid expansion Below 90 Km Middle part	E
1185						110				E
1186						315				E
1189						c 175		1.2		A
1190						250				S
1191						250				E
1192						270				E
1194						70		R		E
1195						330		S		E
1196						(c 158 (Z			Middle part Upper and lower parts	A
1197						270				E
1198						c Z				E
1199						c 270				E
1204						Z			Middle part	E
						(c 140		0.1	Upper part	E
1205						(c 140		0.3	Middle part	E
						(c Z		0.0 ±	Lower part	E
1206						c 225		0.4	Middle part only of original path	E
1207						180		5. ±		Q
1209						c 0		2.5		A
1210						c Z			Or very slow	A
1211						c 90		2.0 +		S
1212						c 90		0.8		A
1214						N/S			Seen from 2 ships	A
1215						(90 (270			Middle part Lower part	E
1216						112				S
1217						45 ±		0.2		E
1218						202				A
1219						90		0.2	4 strata; 1 and 3 prob. Z	E
1220						169			Possibly N	S
1221	119	92							Train 75 Km long; $i = 147^\circ$, $e = 0.74$	E
1222						N/S			9 strata, vel. growing larger with dec. height	S
1224						c 225	133 +	0.8	Assuming 100 Km height	E
1226	142 ±	40 ±				67				A
1227						270				A

NO.	M E T E O R			T R A I N					R E M A R K S	
	H _b	H _e	V	H ₁	H ₂	d	V _t	V _a		
	Km	Km	Km/Sec	Km	Km	o	Km/Hr	o/Min		
1228						180				A
1229						195				A
1230	129	73	39		93	(228	36		5 strata	E
						(45	160		Expansion 13 Km/h	
						180			90 Km height assumed	
1231									5 strata; 1,3,5 to M; 2,4 Z; 3 greatest vel.	S
1233	150	64		(92)					Height of middle part; length of path 100 Km	E
1235						135				A
1236						270?			Lower part longest enduring	A
1237						23	161		Assuming 90 Km height	A
1239						c 0				E
1241						45		S	Uncertain data	S
1243						260			Rapid, 3 strata	S
1246						170			2 parts of train lasted longer	E
1247						168		1.5		S
1249						c 245		1.0	Assuming 90 Km height	A
1251						c 120		2.0		S
1252	96	16				90			Upper levels faster; complicated motions	A
1253						90		S	Drifted as whole?	A
1254						c 315				E
1255						90				E
1256						Z				A
1257						315		S		E
1258						SE/NW			3 strata; apex to SE	S
1259						180 ±			With a vertical component	S
1260						Z ±				A
1262	130	84	77	100	87	(90	111		At 90 Km; train expanded to 4 Km in diam.	E
						(Z	0		at 87 Km	
1263	84					315			Upper part almost stationary	S
1264	159	56	43	122	78	(210		R	122 to 96 Km level; path length 139 Km	S
						(300		R	96 to 78 Km level	
1265						225				S
1266						280		0.5 +		A
1268						50		S		A
1269						145		2.0		A
1271	112	92		(95)		270	90+		Mean height of train	E
1274				(90)		(135	67+		Upper level) height	E
						(135	148+		Lower level) assumed	
1275						135	150		90 Km assumed	E
1276						c 0		0.3		E
1277						(c 75		2.+	Or to 125°; ambiguous; top	S
						(c Z		0.	Bottom	
1278						90				S
1279						(23			Whole train for 3 min.	A
1280						(112			Lower half after 3 min.	
1281						Z?			Spiral; head on	S
						(c 23			Upper part, after division	S
						(c Z			Lower part	
1282						N/S		S	Several parallel currents?	A
1283						288		1.5		S
1284						N/S			At least 2 opposite levels	S
1285						315	160		90 Km height assumed, 3 levels	E
1286						90??	(150)	0.5-	90 Km height assumed	E
1287						225	150	1.2	90 Km height assumed	E
1288						180	105		90 Km height assumed	A
1289						135			3 levels; central part moving	E
1290						305	100		90 Km height assumed	E
1291	153	56		(129)	(62)	down	>160		Initial mean height, final mean height;	A
						(0	155		mean height after 5.5 min. 113 Km	
1292						(202	180		90 Km height	A
						Z			(mean?)	A
1293						(180		1.3	Upper level	A
1296						(180		4.0	Central level	A

NO.	M E T E O R			T R A I N					R E M A R K S	
	H _b	H _e	V	H ₁	H ₂	d	V _t	V _a		
	Km	Km	Km/Sec	Km	Km	o	Km/Hr	o/Min		
1297						135		S	Very small velocity, 2 levels	m
1298						(c 2			Upper part	m
						(c 60		0.3	Lower part	m
1299			*			(c 2 ±			Upper and lower part	m
						(c 67		0.2	Central part	m
1300						225		0.4	All levels equal	m
1302						(2			Upper part	m
						(0			Lower part	m
1307						0			Small central part	m
1309						349				m
1310	186	8		27	17				Path length 478 Km, train 32 Km	m
1315						90				m
1317						135			Upper central part	m
1318						(2			Upper half	m
						(205			Lower half	m
1321						135		S		m
1326						315			Central part	m
1335	77	43	53	77	43	112	204		(Z above 70, below 45 Km motion in 70-45 Km level	m

TABLE III

This table gives the annual and monthly distribution of the trains, along with their total numbers. The influence of the well-known cometary showers is very strongly indicated in the monthly totals.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	-	TOTAL
1801														
2														1
3										1				1
4														
5										1				1
6														
7														
8														
9														
10	1													1
1811					1									1
12								2						2
13											1			1
14									1	1				2
15					1		1							2
16														
17				1										1
18		1						1		1				3
19					1						1			2
20														
1821						1			1					2
22						1		2	1		1			7
23			2					1			1			2
24														
25											2	1		3
26			1											1
27												1		1
28														
29									1					1
30														
1831											1			1
32										1				1
33											11	1		12
34							1		1			1		2
35											1			2
36								1			2			3
37								1						1
38	1		1					1			2			5
39								2						2
40	1				1		1	1						4
1841			1					1	1			1		4
42				1			1	1			1			4
43			1			1								3
44									2					2
45						1	1			1				3
46						2		1	1	2	3			9
47	1				1		1	2		1	2	2		10
48	1		1						1					3
49								2			4	2		8
50	1	3				1	1		1	1	1			9
1851				2	2	2					1			7
1852								1		1	1			3
53								2	1	2		1		6
54				1				2		1	1			5
55	1											2		3
56	1						2	1		1				5
57				1			1				1			3
58							1	3	1		1	1		7
59								6		2	2			10
60	1	1						2						4

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	-	TOTAL
1861			1		1		3	3		1	1			10
62	1	1		2			1		3	1				9
63							1	15	1	2	7			26
64		1			1		1	5	3		1			12
65		3					2			1	4	1		11
66	1					2	1	1		1	32			38
67						1	1	4		1	16	1		24
68						3	1	1	2		25	1		33
69					1	2		1	1		6	1		12
70		1						2	1		3	1		8
1871		2	1	2			1	1	3	1	1	2	1	15
72					1			3		1	8	1		14
73		1			1	2			2	1				7
74								1	2	2		1		6
75		1						1	1	1		1		5
76						1	2	3	2	2	1	1		12
77			1	1				2	2	2	2			8
78	1		1		1		2	3	2		1	1		12
79		3	1					1	1	2				7
80								2	2			1		5
1881										1	1	1		3
82		1			1		1	5	1	1	1			11
83	1				1	1		3		1		1		8
84					1		3		1	1		1		7
85							1				16	1		18
86								1			1	1		3
87			1	1		2	1	1		3				8
88						1	1	2		1	2	1		8
89		1	1					1			2			5
90	1				1	1		2						5
1891							2	4	2	3	3			14
92					1			2		1				5
93			1					2		1	3	2		9
94		1		1			1	4		1				8
95	1			1						1	3	1		7
96	1	2	1		1	3			2		6			17
97	1	2			1					3				7
98	1			1			2	1	1	2	15	1		24
99								4	1	2	2			9
1900	1	1	1	2			3		1	1		4		14
1	1			1			2			3	12	1		21
2	1	1					1		2					6
3					1	2		1		1	4			9
4					1			1		1	5	2		10
5			1			1	1			2	2	2		10
6	3					1	1	2			1	1		9
7		1		1			1		1	1				5
8	1	1		1			1	1		1	2	1		9
9	1	1	1	1	1	1	1	3	1	1	1	2		15
1910		1		1		1		2	2	5	2			14
1911				1	1	1	2		1	1		2		9
12			1	2		2	1	1		1				8
13	1	1				2	1		1	3				9
14	1					1		1		1		1		5
15							1	2		3				6
16	1			2		1	1	1	1	1				8
17				1	1	1	1			3				7
18		1		1	1								1	4
19				1		1				1		1		4

TABLE 1

Measured depth: 300 M Av. True depth: 292.6 M		Measured depth: 800 M Av. True depth: 788.6 M		Measured depth: 1200 M Av. True depth: 1179.0 M	
Temperature difference	Per cent frequency	Temperature difference	Per cent frequency	Temperature difference	Per cent frequency
2.56°-2.57°	22.2	7.80°-7.81°	4.2	10.42°-10.43°	16.0
2.58°-2.59°	22.2	7.82°-7.83°	0.0	10.44°-10.45°	16.0
2.60°-2.61°	33.4	7.84°-7.85°	25.0	10.46°-10.47°	36.0
2.62°-2.63°	22.2	7.86°-7.87°	45.8	10.48°-10.49°	28.0
		7.88°-7.89°	25.0	10.50°-10.51°	4.0

Frequency distributions of temperature differences between protected and unprotected thermometers at measured wire depths of 300, 800, and 1200 meters. Average true depths computed from temperature differences. "Atlantis" Station 3245.

variation at any depth during the entire period of observation was 9 meters and, in this case, errors in computed sampling depths may rarely be expected to exceed 3 meters and those in temperature, 0.02° .

VERTICAL OSCILLATIONS AND TEMPERATURE VARIATIONS AT STATION 3245

In preparing material for analysis, the original temperature data (corrected) of each sampling were individually plotted against depth and scaled both for temperature at standard depths (see Appendix 1) and for depths of standard isotherms. Time variations of temperature at standard depths (Table 2) are considered to result chiefly from internal vertical movements of the water layers, the magnitudes of which are indicated by time variations in depths of standard isotherms (Table 3).

During the twenty-six hours at Stations 3245, temperatures at standard depths (0-1100 meters) varied from 0.32° to 2.25° (Table 2) as a result of vertical displacements of 15 to 56 meters (Table 3). The smaller temperature variations (0.32° - 0.36°) occurred at depths (200-300 meters) where the water column was least stratified and where the vertical displacements were largest (48-56 meters), whereas the larger variations (1.31° - 2.25°) occurred at depths (100-150 meters) characterized by the greater temperature (and density) stratification, and by corresponding smaller vertical displacements (26-48 meters). In the moderately strongly stratified mid-depths, temperature variation of 0.57° to 0.66° , between 500 and 800 meters, corresponded with vertical displacements of 28 to 41 meters, while still deeper, with diminishing temperature (and density) stratification, temperature variations diminished; at 1100 meters (greatest depth

sampled) a variation of 0.24° corresponded to a 47 meter vertical displacement.

General relationships between diurnal temperature ranges at fixed depths (Table 2) and vertical displacements of the water column (Table 3) to vertical distributions of temperature and density (σ_t) and to vertical variations of density ($\Delta\sigma_t/\Delta Z$) are brought out by Fig. 1. Computations of temperature and vertical displacement ranges are affected by randomness of the observations; if measurements had extended over several days a more satisfactory analysis would have been possible (such, for instance, as that carried out on 13 days of continuous observations at Station 3091.³ Nevertheless, it is brought out that the apparent damping of vertical displacements by increased stratification is insufficient to offset increased temperature varia-

TABLE 2

Depth	Average temperature	Maximum temperature	Minimum temperature	Temperature range
0	23.99°	24.55°	23.65°	0.60°
100	21.96°	22.47°	21.16°	1.31°
150	19.29°	21.08°	18.83°	2.25°
200	18.12°	18.30°	17.98°	0.32°
300	17.47°	17.71°	17.35°	0.36°
400	16.52°	16.77°	16.32°	0.45°
500	14.95°	15.31°	14.74°	0.57°
600	13.14°	13.46°	12.83°	0.63°
700	11.04°	11.30°	10.67°	0.63°
800	9.08°	9.30°	8.64°	0.66°
900	7.71°	7.88°	7.56°	0.32°
1000	6.47°	6.79°	6.29°	0.50°
1100	5.73°	5.87°	5.63°	0.24°

Resumé of temperature variations at standard depths for "Atlantis" Station 3245 from 02^h 54^m, January 23 to 04^h 45^m, January 24, 1939 (G.C.T.). Scaled values.

³ Seiwel, H. R. "Daily Temperature Variations in the Western North Atlantic." *Journal du Conseil*, XIV, No. 3, pp. 357-369, 1939.

TABLE 3

Isotherm	Maximum depth	Minimum depth	Range (meters)
23.00°	82.5	42.2	40.3
22.00°	110.0	77.9	32.1
21.00°	151.8	103.3	48.5
20.00°	161.9	124.5	37.4
19.00°	170.0	144.1	25.9
18.00°	254.0	198.0	56.0
17.50°	325.5	278.0	47.5
17.00°	376.5	338.0	38.5
16.50°	423.0	387.0	36.0
16.00°	458.2	422.0	36.2
15.00°	519.8	484.0	35.8
14.00°	572.0	536.2	35.8
13.00°	620.0	591.0	29.0
12.00°	663.8	636.2	27.6
11.00°	715.5	683.0	32.5
10.00°	770.0	731.0	39.0
9.00°	820.0	778.5	41.5
8.50°	852.0	810.0	42.0
8.00°	883.0	867.8	15.2
7.50°	934.0	906.0	28.0
7.00°	979.5	943.0	36.5
6.00°	1086.0	1039.5	46.5

Resumé of time variations in depth of standard isotherms for "Atlantis" Station 3245 from 02^h 45^m, January 23 to 04^h 45^m, January 24, 1939 (G.C.T.). Values scaled for indicated isotherms.

tions at the fixed depths concerned. For instance, the most strongly stratified layer of water, between 100 and 150 meters depth (average vertical variation of σ_t : $\Delta\sigma_t/\Delta Z = 114.97 \times 10^{-4}$ units of σ_t per meter; average vertical variation of temperature: $\Delta T^\circ/\Delta Z = 4.98 \times 10^{-2}$ degrees per meter), was characterized by an average diurnal vertical displacement of 38.5 meters and a corresponding average temperature change of 1.92°. In the more homogeneous water immediately below, between 200 and 300 meters, where average density stratification ($\Delta\sigma_t/\Delta Z = 9.97 \times 10^{-4}$) was reduced to 8.67 per cent of the above and the vertical variation of temperature ($\Delta T^\circ/\Delta Z = 6.7 \times 10^{-3}$ degrees per meter) to 13.5 per cent, the average diurnal vertical displacement of 51.0 meters produced an average temperature variation of only 0.33°. Still deeper, in the thermocline, where, between 500 and 800 meters, density stratification increased ($\Delta\sigma_t/\Delta Z = 17.71 \times 10^{-4}$), 1.78 times and temperature stratification ($\Delta T^\circ/\Delta Z = 19.4 \times 10^{-3}$) 2.89 times the above, the average vertical displacements were reduced to 34.0 meters or 67 per cent of the above and the accompanying average temperature variation increased 1.89 times, or to

0.627°. In the deepest water layers sampled (between 900 and 1100 meters), the average density stratification ($\Delta\sigma_t/\Delta Z = 8.42 \times 10^{-4}$) decreased to 47.5 per cent, and the temperature stratification ($\Delta T^\circ/\Delta Z = 9.73 \times 10^{-3}$) to 50.2 per cent of its former value, but the average vertical displacement increased 1.15 times to 39.0 meters, producing an average diurnal temperature variation of only 0.390°. These interrelationships are similar to those in other North Atlantic⁴ areas and it may be inferred that the more homogeneous layers of the ocean basins (to depths of approximately 1200–1400 meters) are characterized by relatively larger vertical displacements and smaller diurnal temperature variations.

HARMONIC ANALYSIS OF ISOTHERM-DEPTH VARIATIONS

Results of harmonic analysis of depth variations of selected isotherms for 24 and 12 lunar hour components are tabulated in Table 4 as values of the coefficients, C and α , thus:

$$H = C_0 + C_1 \cos \frac{2\pi}{24} (t - \alpha_1) + C_2 \cos \frac{2\pi}{12} (t - \alpha_2).$$

Phases and amplitudes were determined by least squares,⁵ the former (in lunar hours) having been adjusted to refer from the time of the previous upper transit of the moon at the Greenwich meridian which occurred at 13^h 32.3^m (G.C.T.) on January 22, 1939. Thus analyses were made of the observational series, beginning 14 lunar hours (03^h 57^m, January 23, 1939, G.C.T.) after the time of the moon's upper transit at the Greenwich meridian on January 22 and ending 14 lunar hours (04^h 40^m, January 24, 1939) after its upper transit the following day, January 23 (14^h 14^m; G.C.T.). Consequently the phase angles recorded in Table 4 have been increased by 14 lunar hours, this procedure being preferable to referring the phase to some arbitrary time, even though the coefficients do not necessarily

⁴ Seiwel, H. R. "Time Variability of Hydrographic Elements Determining the Dynamic Situation in the Western North Atlantic." *Proceedings of American Philosophical Society*, LXXXII, No. 3, pp. 369–394, 1940.

⁵ Seiwel, H. R. "Short Period Vertical Oscillations in the Western Basin of the North Atlantic." *Papers in Physical Oceanography and Meteorology*, V, No. 2, 44 pp., 1937.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	-	TOTAL
1920	1				1	2	1	1	1		1			8
21				2					1					3
22									1		3	1		5
23								1	2	1				4
24	1			1	3	2				1	1			9
25	1		1		1	1	1	1	1	2		1		10
26		1			1	2		1	3	2	2			12
27			1				3		2	4	5	2		17
28	2	1		4	1	1	2	2		7	24	1		45
29	2	1		1	1		2	4	1		2	1		15
1930		1			1	3	5	1	2	1	21	1		36
31		1	2	1	1	2	2	3	2	2	54	3		73
32	1	1	1	2	1	1	2	3	1	1	16	3		33
33	1		1		3		1	1	2	9	5	2		25
34					2	3	1	6	2	8	4	1		27
35	1	1	1		2	2	7	2	3	4	3	2		28
36				1			4	15	6	9	3	2		40
37	1	1	1		1	5		8	2	4	3	2		28
38		2	1			2	3			4	3			15
39	1			3	2		2	5	3	9	4		1	30
1940			1	2				4	1	1				9
41	1	1												2
1801)														
1941)	42	44	30	47	47	69	92	190	95	157	388	77	3	1,281
Before)														
1801)	2	2	6	5	4	5	5	2	6	7	4	6	1	55
TOTAL	44	46	36	52	51	74	97	192	101	164	392	83	4	1,336

The writer desires to express his sincere appreciation for a grant from the J. Lawrence Smith Fund of the National Academy of Sciences for aid in the preparation of this paper.

AN ANALYSIS OF VERTICAL OSCILLATIONS IN THE SOUTHERN NORTH ATLANTIC¹

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Contribution No. 276 from the Woods Hole Oceanographic Institution

ABSTRACT

Hydrographic materials for the present analysis consisted of 28 repeated samplings of the water column, each comprising 17 observations between surface and approximately 1100 meters depth, obtained while "Atlantis" was anchored for 26 hours in 5000 meters depth at 25° 32' N, 53° 45' W (Station 3245). The temperature at fixed depths varied as much as 2.25° during the observation period owing to internal vertical displacements of the water layers. Smaller temperature variations (0.32°–0.36°) occurred at depths of 200–300 meters where the water column was least thermally stratified and where vertical displacements were largest (48–56 meters), whereas the larger variations characterized depths of greater thermal stratification.

Analytical transformation of the observational materials by harmonic analysis of vertical displacements of 22 selected isotherms, and subsequent statistical treatment reveals that vertical displacements are well represented by coefficients of 24 and 12 lunar hour frequencies. The effects of irregular influences are largely eliminated and characteristic space properties of the phenomenon are brought out by plotting phases and amplitudes in harmonic diagrams and investigating the geometric properties of the resulting point aggregates. Both diurnal and semidiurnal groups of points were characterized by marked ellipticities and the small, but significant, average vectors of vertical displacements (between surface and 1050 meters) result from combinations of larger amplitudes but of nearly opposite phases. Formulas for computation of ellipse constants, tests for significance of correlation coefficients and average vectors are given in forms suitable for numerical computation.

Statistical analysis of theoretical Internal Waves contingent in the water mass at Station 3245, computed from Fjeldstad's Internal Wave theory, reveals that significant properties of observed displacements are well represented by the theoretical mechanism. Additional geophysical significance is furnished by the phase and amplitude relations of displacement vectors, being such as to suggest a connection between Internal Wave and tidal mechanisms. Internal Wave propagation velocities in the North Atlantic, where depths exceed the average, may be approximated by dividing 221 by the wave order (1st, 2nd, etc.). Length of the first order semidiurnal Internal Wave, having a propagation velocity of 221 cm sec.⁻¹, is 99.05 kms, or approximately 1/100 the length of the semidiurnal tidal wave at the mean depth of the oceans.

¹ Research aided by a grant from the Penrose Fund of the American Philosophical Society.

INTRODUCTION

INTERNAL vertical oscillations in the sea are revealed by time variations of temperature and salinity at fixed points throughout the ocean space. For adequate description of the phenomenon, numerous observations need to be transformed and reduced to patterns appropriately indicating their average state and time variability. The present analysis of approximately 500 repeated temperature measurements, has been undertaken by means of numerical methods adapted from other somewhat analogous geophysical investigations. The procedure represents a departure from customary treatments of oceanographic data; the initial descriptive discussion of observational material is followed by harmonic analyses of the vertical displacements at critical depths, and the results of the transformation then treated statistically. The final part of the paper considers comparisons of statistical properties of observed and theoretical vertical displacements and the possible relation of Internal Wave to tidal phenomena.

The basic information analyzed was obtained from 28 repeated temperature samplings² of the water column taken uninterruptedly at 17 sub-surface levels (to 1200 meters depth) over 26 hours (02^h 54^m, January 23 to 04^h 45^m, January 24, 1939, G.C.T.) while the "Atlantis" was anchored in 5000 meters depth at Station 3245 (25° 32' N, 53° 45' W). Due to favorable weather and absence of drift, the measurements (taken with the usual precision) were treated as having a high degree of reliability. Depths of observations changed but little between successive samplings, as evidenced by frequency distributions of temperature differences (ΔT°) between protected and unprotected thermometers (Table 1) for measured wire lengths of 300, 800, and 1200 meters. The maximum computed

² Salinity values were determined by chemical titration of three complete samplings.

apply outside of the original observation period. The results of harmonic analyses of vertical displacements for 6 isotherms are illustrated by Fig. 2.

In general, vertical variations of phase angles, amplitudes and ratios of amplitudes (C_{24}/C_{12}) are identified with the internal structure of the water column in that vertical transitions closely coincide with temperature and density stratification (Fig. 1, Table 4). In the upper strongly stratified part of the water column, approximately between 50 and 150 meters, the phase of both waves change rapidly with depth; amplitudes of both waves were relatively low with the semi-diurnal wave dominating, (average $C_{24}/C_{12} = 0.648$). Somewhat deeper, in the more homogeneous water between 150 and 450 meters, both 24 and 12 hourly waves maintained more nearly uniform phase angles and the amplitudes of both waves attained maximum values, with the 12 hour amplitude again dominating (average $C_{24}/C_{12} = 0.525$). In still deeper water of increased stability, as between 550 and 1050 meters (Fig. 1), vertical variation of phase angles again increased and amplitudes were, on the whole, diminished, but the lunar diurnal wave generally dominated.

TABLE 4

Isotherm	C_0	C_{24}	α_{24}	C_{12}	α_{12}	C_{24}/C_{12}
23.0°	62.52	5.39	23.39 ^h	5.56	7.08 ^h	0.97
22.0°	99.28	4.56	22.56 ^h	5.09	7.71 ^h	0.901
21.0°	118.74	0.84	7.50 ^h	6.72	8.45 ^h	0.125
20.0°	135.11	0.94	11.20 ^h	2.04	8.96 ^h	0.461
19.0°	157.58	2.48	12.07 ^h	2.53	1.01 ^h	0.980
18.0°	216.46	13.33	15.73 ^h	11.01	3.36 ^h	1.211
17.5°	295.80	5.41	15.86 ^h	10.27	2.66 ^h	0.527
17.0°	356.79	2.85	17.89 ^h	11.21	3.15 ^h	0.254
16.5°	400.76	2.43	15.23 ^h	8.52	3.75 ^h	0.285
16.0°	434.22	4.42	13.17 ^h	15.34	3.58 ^h	0.288
15.0°	497.08	4.01	13.53 ^h	12.82	2.65 ^h	0.313
14.0°	555.24	1.57	16.00 ^h	11.82	2.43 ^h	0.133
13.0°	607.66	1.03	2.12 ^h	5.78	3.72 ^h	0.178
12.0°	653.18	3.87	17.65 ^h	2.76	4.29 ^h	1.40
11.0°	702.23	4.69	17.60 ^h	5.12	5.48 ^h	0.916
10.0°	755.36	8.28	7.00 ^h	4.22	4.85 ^h	1.962
9.0°	805.28	6.88	11.46 ^h	5.02	3.97 ^h	1.371
8.5°	835.32	7.82	14.53 ^h	3.33	4.92 ^h	2.348
8.0°	875.05	2.79	21.44 ^h	1.21	2.58 ^h	2.306
7.5°	918.95	6.54	0.76 ^h	1.21	3.64 ^h	5.405
7.0°	956.95	4.24	21.03 ^h	9.36	11.16 ^h	0.453
6.0°	1057.45	11.87	22.85 ^h	8.24	11.53 ^h	1.44

Lunar diurnal and lunar semidiurnal coefficients of observed vertical displacements of isotherms at "Atlantis" station 3245.

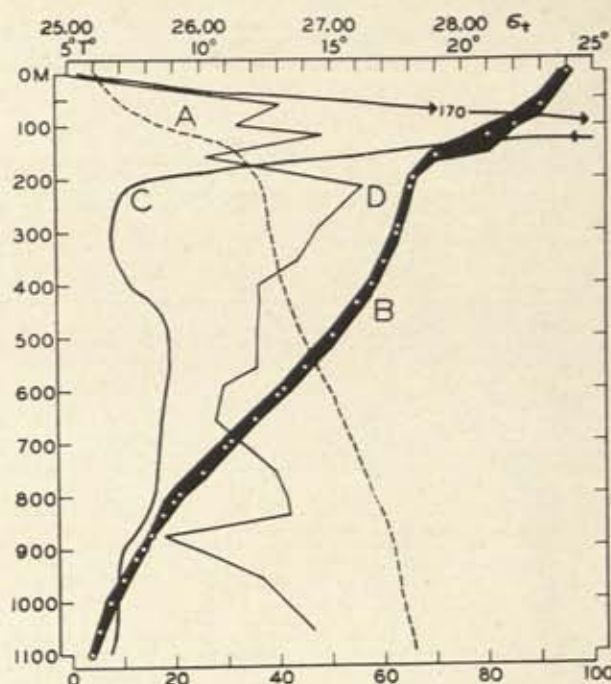


FIG. 1. "Atlantis" Station 3245. 02^h 54^m, January 23 to 04^h 45^m, January 24, 1939 (G.C.T.). A = average vertical distribution of density (σ_t); B = average vertical distribution of temperature, variation at fixed depths indicated by width of ribbon; C = average vertical rate of change of density per meter, $\Delta\sigma_t/\Delta Z$; D = vertical displacements of water column during observation period (referred to bottom scale, meters).

THE APPARENT DOMINANCE OF 24 AND 12 LUNAR HOUR PERIODS IN VERTICAL OSCILLATIONS OF THE WATER COLUMN

(a) Examination of Residues after Extraction of 24 and 12 Lunar Hour Waves

As a possible means of estimating the dominance of 24 and 12 lunar hour periods in vertical oscillations of the water layers (Table 4), the residues, after extraction of these waves from original observed vertical displacements of isotherms, were combined into a single frequency distribution (Table 5) and tested for normality. This procedure is used since the normal curve, having been mathematically deduced as the distribution resulting from combination of an infinite number of small random errors, has a fundamental status, and a quantity, such as the above, distributed according to this law may be the result of uncontrolled chance causes. On the other hand, if the distribution of residues

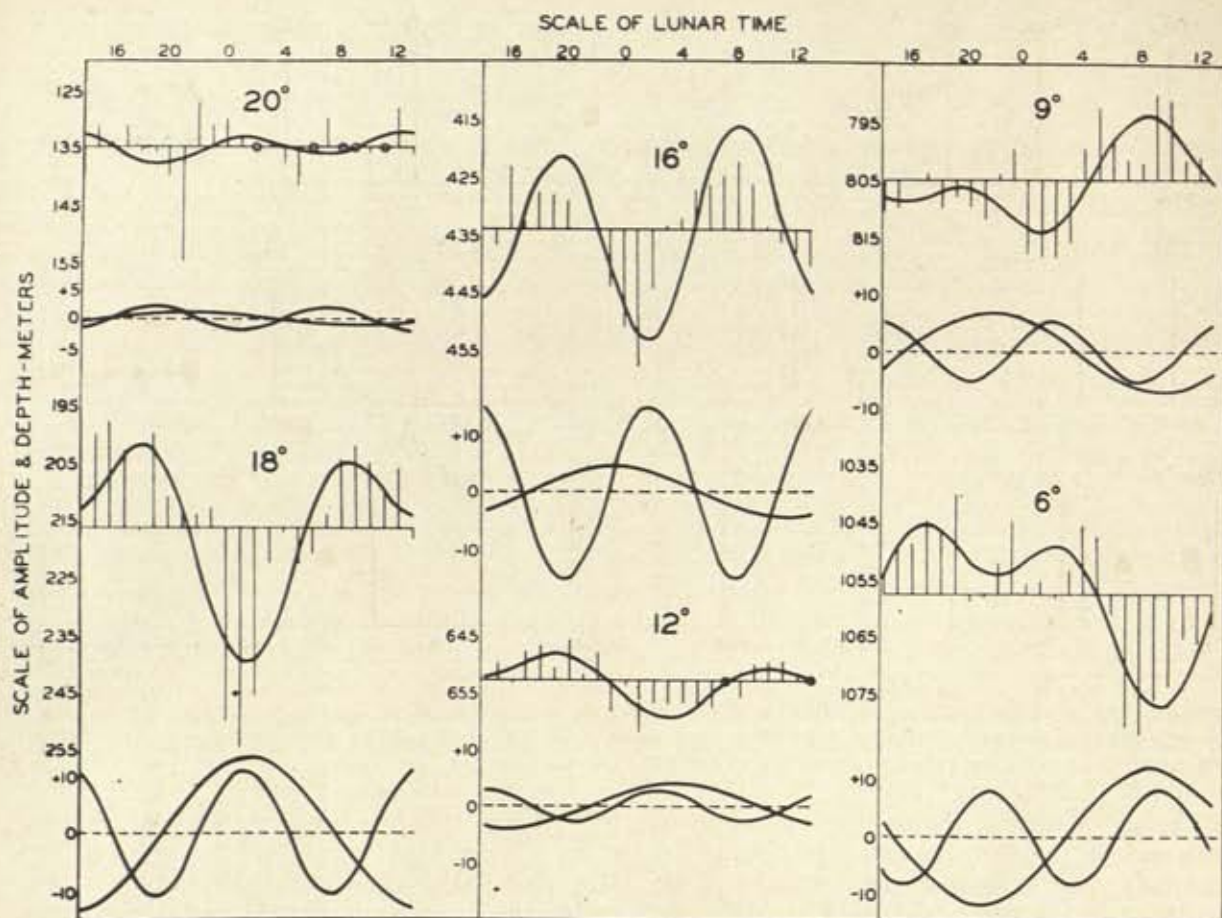


FIG. 2. Harmonic analysis of vertical displacements of 20°, 18°, 16°, 12°, 9° and 6° isotherms, Station 3245. Observed vertical displacements shown as departures from mean values to which are fitted curves based on sums of computed lunar diurnal and lunar semidiurnal sine waves—also shown separately. Time scale in lunar hours, 0^h representing moon's upper transit at Greenwich meridian on January 23, 1939 (14^h 14^m, G.C.T.).

should be non-normal, it may be inferred that they are not all the result of chance, and quite possibly contain an additional geophysical controlled oscillation. Naturally, this use of the normal distribution is to some extent open to question and like any application of probability theory needs to be considered with a "grain of salt," and the result may be chiefly empirical. However, in the absence of more definite information, it seems reasonable that its use as a test for randomness in the data under consideration should give basic information on the nature of the controlling geophysical phenomenon.

The frequency distribution of residues resulting after subtraction of combined 24 and 12 lunar hour waves from the original vertical displacements of 22 isotherms is given in Table 5. The first four corrected movements about the mean

(using Bernoulli class marks) are:

$$\begin{aligned}\mu_1 &= 0 \\ \mu_2 &= 1.93182 \\ \mu_3 &= 0.20417 \\ \mu_4 &= 13.54395,\end{aligned}$$

and the following statistics for testing normality of the distribution are:

$$\begin{aligned}\sigma &= \sqrt{\mu_2} = 1.389899 \\ \beta_1 &= \frac{\mu_3^2}{\mu_2^3} = 0.005782 \\ \gamma &= \sqrt{\beta_1} = 0.07603 \\ \beta_2 &= \frac{\mu_4}{\mu_2^2} = 3.629209 \\ \omega_n' &= 0.81622\end{aligned}$$

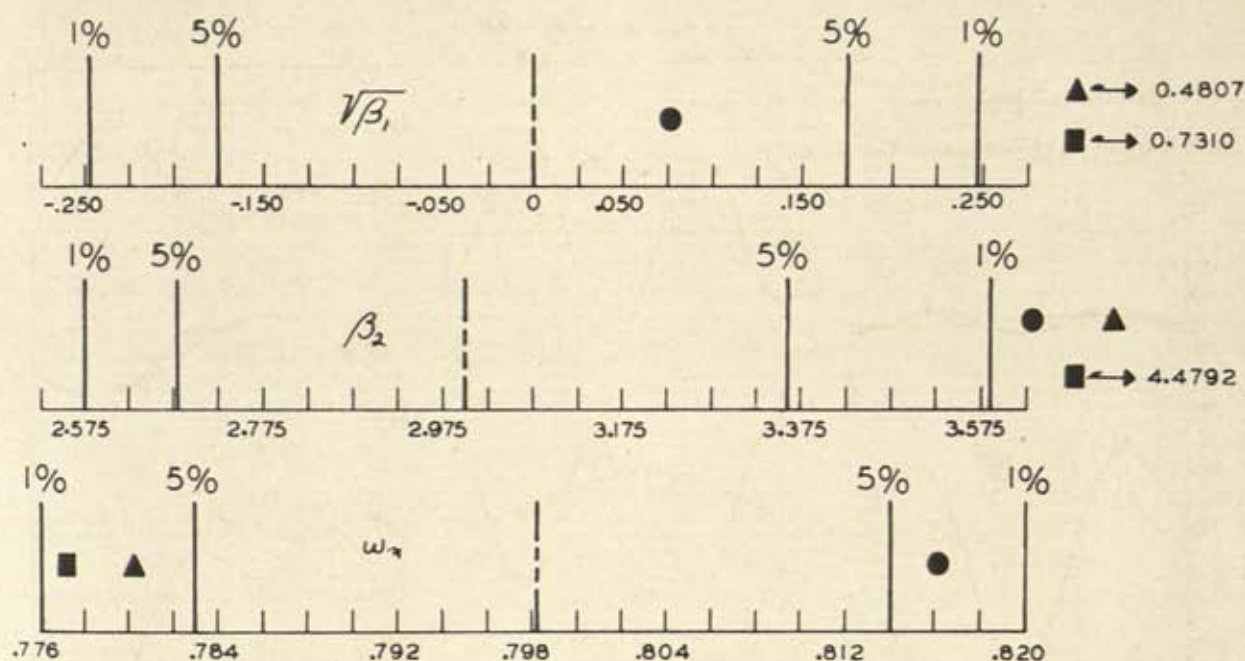


FIG. 3. 5 per cent and 1 per cent probability limits for a random sample of 528 individuals drawn from a normal population. Values for frequency distribution of residues after subtraction of 24 and 12 lunar hour waves = ●; for original frequency distribution of departures from mean = ■; and for frequency distribution of residues after subtraction of 12 pendulum hour and 12 lunar hour combination = ▲.

(ω_n' being the ratio of the mean to the standard deviation of the distribution). In testing for departure from normality, two separate tests, one regarding skewness and the other kurtosis, are generally used. To detect lack of symmetry (skewness), the $\sqrt{\beta_1}$ appears to be a suitable criterion,⁶ and tables of 5 per cent and 1 per cent levels⁷ are generally believed to be sufficiently accurate for ordinary purposes. For tests of platykurtic or leptokurtic properties, Pearson suggests the ω_n' test of R. C. Geary⁸ as being preferable to the β_2 test, since the distribution of the latter, particularly for small samples, is not well known.

Results of all three tests for normality ($\sqrt{\beta_1}$, β_2 , ω_n') applied to the foregoing frequency distribution are given by Fig. 3. The value of $\sqrt{\beta_1} = 0.07603$ for $n' = 528$ is well above the 5 per cent probability level; $\beta_2 = 3.629$ falls a

little below the 1 per cent level whereas the value $\omega_n' = 0.81622$ for $n' = 528$, according to Geary's (1935) table F, falls about midway between the 5 per cent (0.814) and 1 per cent (0.820) probability levels.

Hence, it appears that the distribution of residues is random, or sufficiently so to suggest that for practical purposes (in the absence of more pertinent information) the vertical oscillation mechanism of the water column at the station investigated may be considered as being

TABLE 5

Class interval (meters)	Frequency
-20.0 to -16.1	2
-16.0 to -12.1	7
-12.0 to -8.1	30
-8.0 to -4.1	79
-4.0 to -0.1	147
0.0 to 3.9	142
4.0 to 7.9	89
8.0 to 11.9	21
12.0 to 15.9	8
16.0 to 19.9	2
20.0 to 23.9	1
	528

⁶ Pearson, E. S. "A Comparison of β_2 and Mr. Geary's Criteria." *Biometrika*, XXVII, Memoir XII, Section II, pp. 333-352, 1935.

⁷ Tables for Statisticians and Biometricians. Part II, Table XXXVII bis, page 224. Biometric Laboratory, University of London.

⁸ Geary, R. C. "Introduction of the Ratio ω_n' and its Distribution." *Biometrika*, XXVII, Memoir XII, Section I, pp. 310-332, 1935.

TABLE 6

Isotherm	C ₀	C ₁	α_1	C ₂	α_2
23.00°	63.88	6.44	11.73	5.25	9.45
22.00°	99.53	6.50	11.96	5.33	10.19
21.00°	117.77	2.53	12.83	3.32	11.38
20.00°	134.48	2.00	10.92	2.01	11.52
19.00°	157.23	3.02	9.12	0.97	3.42
18.00°	215.13	14.13	5.20	9.68	5.34
17.50°	295.73	4.36	7.76	14.91	5.51
17.00°	358.07	3.31	13.36	12.87	4.58
16.50°	402.42	2.79	3.32	11.67	4.41
16.00°	436.19	4.39	1.19	9.90	4.66
15.00°	498.48	2.09	5.50	10.27	5.19
14.00°	555.09	4.78	12.10	8.16	5.70
13.00°	607.28	5.43	12.87	5.47	5.56
12.00°	654.68	6.17	7.69	1.91	6.42
11.00°	703.42	7.53	8.16	4.41	7.85
10.00°	755.69	5.36	20.82	5.01	6.83
9.00°	805.60	2.43	27.45	5.17	6.03
8.50°	836.34	5.61	5.20	2.94	7.22
8.00°	875.76	4.62	12.03	1.34	3.76
7.50°	917.83	7.73	14.79	1.57	5.01
7.00°	957.15	2.39	14.03	9.71	1.03
6.00°	1056.29	10.38	12.76	9.32	1.40

Results of harmonic analysis of observed vertical displacements of isotherms at "Atlantis" Station 3245 for periods of 12 pendulum hours and of 12 lunar hours.

dominated by frequencies of 12 and 24 lunar hours.

Application of the Chi squared test for goodness of fit to the normal frequency curve best fitting the data:

$$F = \frac{528}{1.3899} \frac{1}{\sqrt{2\pi}} e^{-\frac{1}{2} \left(\frac{X-0.4981}{1.3899} \right)^2}$$

(where X is the Bernoulli class mark: 0, 1, 2, 3, ... n) gives satisfactory results. Grouping frequencies less than 7, at the tails of the curve, the value of the Chi squared function is:

$$\chi^2 = \frac{(F_1 - f_1)^2}{F_1} + \frac{(F_2 - f_2)^2}{F_2} + \dots + \frac{(F_n - f_n)^2}{F_n} = 6.34497$$

(where F is the theoretical and f the observed frequency). Computation was based on 8 groups (after clubbing frequencies at the tails of the curve); in fitting the Gaussian curve, 3 constants are fixed (total, mean and standard deviation) so that 5 (n) degrees of freedom remain. Hence, entering Elderton's tables⁹ at $n' = 6$

⁹ Tables for Statisticians and Biometricians. Part I, Table XII.

($n' = n + 1$), the value of the Pearson probability is:

$$P = 0.2767,$$

from which may be concluded that in 27.7 times out of 100 we should get in random sampling a fit as bad, or worse, if the real distribution were Gaussian.

(b) Examination of Original Frequency Distribution

The foregoing frequency distribution of residues is now compared with the distribution composed of observed vertical displacements of identical isotherms, expressed as departures from mean values before the extraction of the 24 and 12 lunar hour waves. The size of the sample is, of course, the same; the first four corrected movements about the mean (using Bernoulli class marks):

$$\begin{aligned}\mu_1 &= 0 \\ \mu_2 &= 4.49913 \\ \mu_3 &= 6.97801 \\ \mu_4 &= 90.66770\end{aligned}$$

were used to compute the following statistics:

$$\begin{aligned}\sigma &= \sqrt{\mu_2} = 2.1211 \\ \beta_1 &= \frac{\mu_3^2}{\mu_2^3} = 0.53467 \\ \gamma &= \sqrt{\beta_1} = 0.73100 \\ \beta_2 &= \frac{\mu_4}{\mu_2^2} = 4.47916 \\ \omega_n' &= 0.7773.\end{aligned}$$

Values for $\sqrt{\beta_1}$, β_2 and ω_n' entered in the chart (Fig. 3) of their probability limits for $n' = 528$ definitely indicate a non-normal distribution; in particular the controlled oscillations in the distribution causes an extreme skewness to the left ($\sqrt{\beta_1} = 0.53467$).

(c) Examination of Residues after Extraction of a 12 Pendulum Hour Wave and a 12 Lunar Hour Wave

The foregoing application of probability theory to the analysis of vertical oscillations of the water column permits the inference that (on the basis of existing evidence) the observed oscillations are well described by lunar diurnal and lunar semi-diurnal periods, plus residual motions resulting from random causes. Because of the brief observational series, as well as theoretical restrictions on the analytical methods, conclusions of

more theoretical or more practical value are not at present permissible. However, since it has been suggested that vertical displacements may exist as free inertial motions having periods of 12 pendulum hours, it is desirable to reexamine the original data from this point of view and to make a comparison with the results of the foregoing analysis.

Thus, at the latitude of Station 3245, ($\varphi = 25^\circ 32' N$) the length of one half pendulum day, or 12 pendulum hours $= \frac{12}{\sin \varphi} = 27.84$ sidereal hours, and the period of an inertia wave (12 pendulum hours) will be only 3.14 sidereal hours in excess of that of a lunar diurnal wave (24.70 sidereal hours) and could not be decisively separated by harmonic analysis of so short an observational series as that under consideration. Values of the coefficients:

$$H = C_0 + C_1 \cos \frac{2\pi}{27.84} (t - \alpha_1)$$

for a possible 12 pendulum hour component in vertical displacements of isotherms are tabulated in Table 6; phase angles (in sidereal hours) are adjusted to refer from 0^h Greenwich (January 23, 1939), although the analyses were actually carried out on an observational series which began 3 hours later (03^h 00^m, G.C.T., January 23, 1939).

After extraction of a 12 pendulum hour wave from the original observations of vertical displacements of isotherms, examination of the residues indicated the presence of an additional wave having a period length of approximately 12 lunar hours (such as would be expected because of small differences in period lengths of the inertia and lunar diurnal components at this latitude). Thus, a second harmonic analysis was carried out on the 22 residues, the results of which are tabulated as coefficients of a second lunar semidiurnal component:

$$C_2 \cos \frac{2\pi}{12.353} (t - \alpha_2)$$

in Table 6; phase angles also given in sidereal hours, refer to 0^h Greenwich (January 23, 1939) as before. Amplitudes both of the 12 pendulum hour and 12 lunar hour waves of this second computation differ by small amounts only from those previously computed for the lunar diurnal and lunar semidiurnal waves (Table 4), and as a means of estimating which of the two combinations of components best represent the observed

TABLE 7

Class interval (meters)	Frequency
-20 to -16.1	1
-16 to -12.1	3
-12 to -8.1	32
-8 to -4.1	104
-4 to -0.1	155
0 to 3.9	129
4 to 7.9	76
8 to 11.9	19
12 to 15.9	4
16 to 19.9	3
20 to 23.9	1
24 to 27.9	1
	<hr/> 528

vertical displacements, the final residues, after extraction of the latter combination, were analyzed as before.

The frequency distribution of residues resulting after subtraction of the combination of a 12 pendulum hour wave and a 12 lunar hour wave from the vertical displacements of the 22 isotherms as given in Table 7 has the same class intervals as that for the frequency distribution of residues in Table 5. The first four moments about the mean are:

$$\begin{aligned}\mu_1 &= 0 \\ \mu_2 &= 2.02727 \\ \mu_3 &= 1.38742 \\ \mu_4 &= 15.29430,\end{aligned}$$

and the following statistics are computed for the distribution:

$$\begin{aligned}\sigma &= 1.4238 \\ \beta_1 &= 0.23104 \\ \gamma &= 0.48066 \\ \beta_2 &= 3.7214 \\ \omega_n' &= 0.7803.\end{aligned}$$

Values of $\sqrt{\beta_1}$, β_2 and ω_n' entered in the chart of probability limits for a sample of 528 individuals (Fig. 3) clearly show that the distribution under consideration is not normal. The statistical characteristics of dispersion, skewness and kurtosis characterizing the original frequency distribution of observed displacements of isotherms, while significantly reduced by extraction of inertia and lunar semidiurnal components, still indicate significant departures from normality. In particular, the strong asymmetry of the present distribution is decisive in deciding its non-normality. Hence, in the present case, vertical oscillations of water layers are far better represented by the combination of lunar diurnal and lunar semidiurnal waves than by a combina-

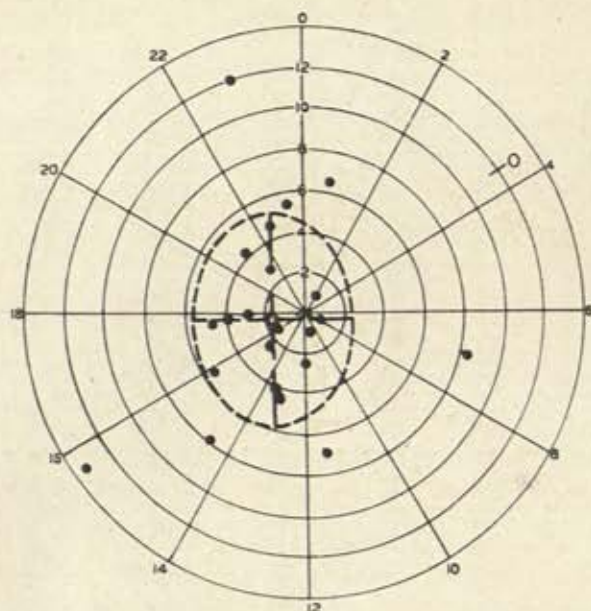


FIG. 4. Harmonic dial for 24 lunar hourly sine wave in diurnal variations of vertical displacements of 22 isotherms at "Atlantis" Station 3245 (25° 32'N, 53° 45'W), and 50 per cent probable ellipse. Scale refers from moon's upper transit at Greenwich (13^h 32^m, January 22, 1939), and inner 0 indicates moon's upper transit at meridian of Station 3245 (17^h 14^m, January 22, 1939. G.C.T.). Each dot marks an isotherm, length of vector from center gives amplitude (in meters) and its direction, the phase in lunar hours.

tion of a 12 pendulum hour and a lunar semi-diurnal wave, thus justifying the use of the former combination for future discussion. For the present, the physical significance of this inference remains problematical.

SPACE VARIABILITY OF THE LUNAR DIURNAL AND LUNAR SEMIDIURNAL COMPONENTS

Since the lunar diurnal and lunar semidiurnal components of vertical oscillations of the water column are specified completely by amplitudes and the times of maxima (phase angles), the sine and cosine function of each frequency have been combined into sine waves with amplitudes, C , and phases, α . Thus:

$$X \cos \alpha + Y \sin \alpha = C \cos (\alpha - \alpha)$$

with:

$$X = C \sin \alpha$$

$$Y = C \cos \alpha$$

$$C^2 = X^2 + Y^2$$

$$\tan \alpha = \frac{X}{Y}$$

The relations for each frequency are conveniently illustrated by plotting in polar coordinate (the "harmonic dial" of Bartels¹⁰); each point then has the coordinates C and α , the lengths of the vector being C and its azimuth, α . Thus N sets of harmonic coefficients may be represented on each dial as a group of N points (Figs. 4, 5, 6 and 7) and the space variability of the vertical oscillations so represented may be transferred into the geometric properties of the group. In the plane coordinate system each point has the rectangular coordinates X_ν , Y_ν ($\nu = 1, 2, 3, \dots, n$), and the coordinates of the center C (X_0 , Y_0) are:

$$X_0 = \Sigma X_\nu / N$$

$$Y_0 = \Sigma Y_\nu / N.$$

We also have:

$$\sigma_x^2 = \frac{\Sigma (X_\nu - X_0)^2}{N}$$

$$\sigma_y^2 = \frac{\Sigma (Y_\nu - Y_0)^2}{N}$$

$$r\sigma_x\sigma_y = \frac{\Sigma (X_\nu - X_0)(Y_\nu - Y_0)}{N},$$

where r is the usual correlation coefficient between X_ν and Y_ν . The general Gaussian frequency distribution (normal correlation surface) which has the equation:

$$df = \frac{N}{2\pi\sigma_x\sigma_y\sqrt{1-r^2}} e^{-\frac{1}{2(1-r^2)}\left(\frac{x^2}{\sigma_x^2} + \frac{y^2}{\sigma_y^2} - 2r\frac{xy}{\sigma_x\sigma_y}\right)} dx dy$$

(where X and Y are variants, measured as deviations from their means X_0 and Y_0) and which best fits the cloud of points (judged by least squares) is to be computed.

The formulae used in the computation are given in a form suitable for numerical computation.¹¹ The value of:

$$\frac{1}{1-r^2} \left(\frac{X^2}{\sigma_x^2} + \frac{Y^2}{\sigma_y^2} - \frac{2rXY}{\sigma_x\sigma_y} \right) = \text{constant}$$

and the lines of equal frequency are ellipses with center at C . The major axis of the ellipse is inclined toward the X axis by θ where:

$$\tan 2\theta = \frac{2r\sigma_x\sigma_y}{\sigma_x^2 - \sigma_y^2}$$

¹⁰ Bartels, J. "Statistical Methods for Research on Diurnal Variations." *Terrestrial Magnetism and Atmospheric Electricity*, XXXVII, No. 3, pp. 291-302, 1932.

¹¹ Reference footnote 10.

and lies between 0° and 90° when $r > 0$, between 90° and 180° when $r < 0$; for $r = 0$, $\theta = 0$ when $\sigma_x > \sigma_y$, and 90° when $\sigma_x < \sigma_y$. When $\sigma_x = \sigma_y$, the ellipses degenerate into circles.

The average square distance (M) of each point from the center, C , has been termed by Bartels the "two dimensional standard deviation," thus:

$$M^2 = \frac{(X_r - X_0)^2 + (Y_r - Y_0)^2}{N}$$

and is useful in measuring dispersion of the group of points.

In the case of a perfect Gaussian distribution, the total probability that a point falls outside the ellipse is:

$$e^{-\frac{1}{2(1-r^2)}\left(\frac{X^2}{\sigma_x^2} + \frac{Y^2}{\sigma_y^2} + \frac{2rXY}{\sigma_x\sigma_y}\right)}$$

The probable ellipse surrounding $N/2$ points both inside and outside is:

$$e^{-\frac{1}{2(1-r^2)}\left(\frac{X^2}{\sigma_x^2} + \frac{Y^2}{\sigma_y^2} + \frac{2rXY}{\sigma_x\sigma_y}\right)} = \frac{1}{2},$$

its semi-major (P_1) and semi-minor (P_2) axes

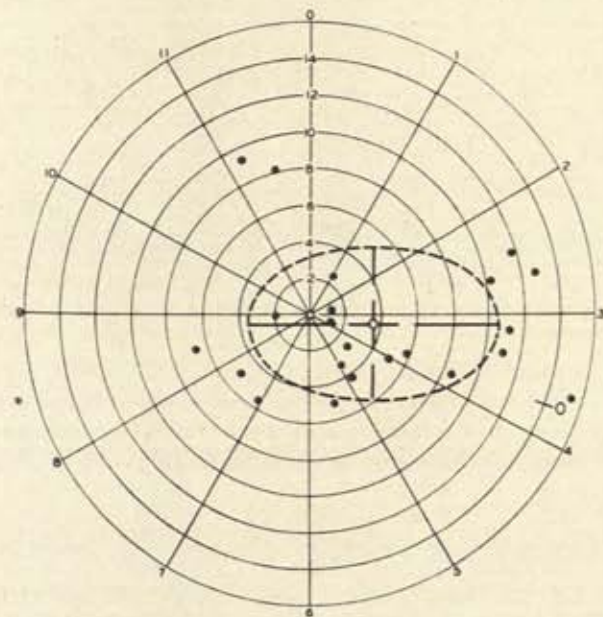


FIG. 5. Harmonic dial for 12 lunar hourly sine wave in diurnal variations of vertical displacements of 22 isotherms at "Atlantis" Station 3245 ($25^\circ 32'N$, $53^\circ 45'W$), and 50 per cent probable ellipse. Scale refers from moon's upper transit at Greenwich ($13^h 32^m$, January 22, 1939), and inner 0 indicates moon's upper transit at meridian of Station 3245 ($17^h 14^m$, January 22, 1939, G.C.T.). Each dot marks an isotherm, length of vector from center gives amplitude (in meters) and its direction, the phase in lunar hours.

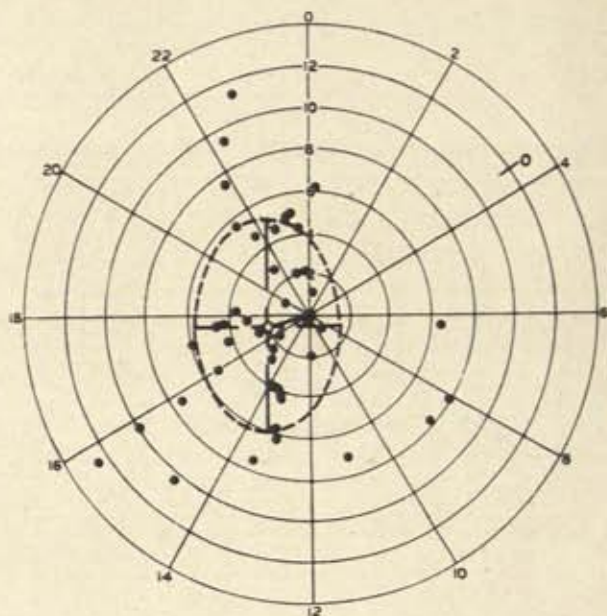


FIG. 6. Harmonic dial for 24 lunar hourly sine wave in diurnal variations of vertical displacements at forty-three 25 meter intervals (over a depth of 1050 meters) based on scaled phase and amplitude relations (see text) at "Atlantis" Station 3245. The 50 per cent probable ellipse and average vector are shown. Scale refers from moon's upper transit at Greenwich ($13^h 32^m$, January 22, 1939) and inner 0 indicates moon's upper transit at meridian of Station 3245 ($17^h 14^m$, January 22, 1939, G.C.T.). Each dot marks a depth, length of vector from center gives amplitude (in meters) and its direction, the phase in lunar hours.

being:

$$P_1, P_2 = 0.83256\sqrt{(\sigma_x^2 + \sigma_y^2) \pm \sqrt{(\sigma_x^2 - \sigma_y^2) + 4r^2\sigma_x^2\sigma_y^2}}$$

Also, in general:

$$\sqrt{P_1^2 + P_2^2} = 1.1774M.$$

Since the formulae give constants of a Gaussian distribution which best fit the group of points without presupposing that the group itself is Gaussian, values may always be computed. As a partial test of normality the number of points inside and outside the probable ellipse should be nearly equal.

Harmonic dials in which phases and amplitudes of lunar diurnal and lunar semidiurnal components of vertical oscillations of 22 isotherms (Table 4) are represented as single points and, the 50 per cent probability ellipses fitting each group of points, are illustrated by figures 4 and 5. The ellipses represent both distributions fairly

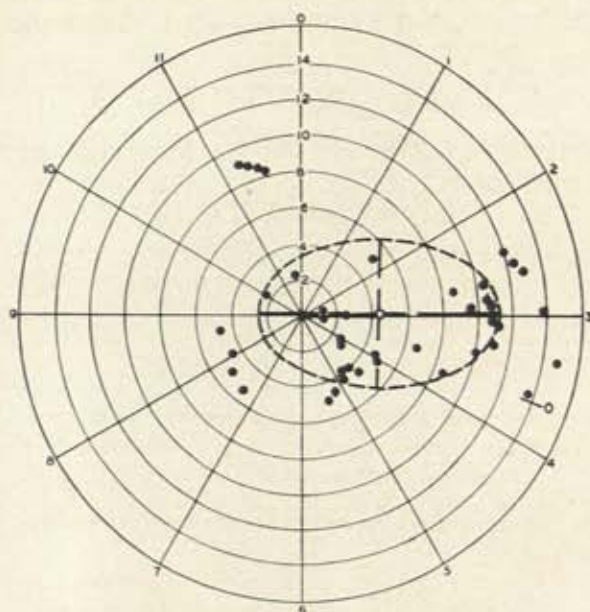


FIG. 7. Harmonic dial for 12 lunar hourly sine wave in diurnal variations of vertical displacements at forty-three 25 meter intervals (over a depth of 1050 meters) based on scaled phase and amplitude relations (see text) at "Atlantis" Station 3245. The 50 per cent probable ellipse and average vector are shown. Scale refers from moon's upper transit at Greenwich ($13^h 32^m$, January 22, 1939) and inner 0 indicates moon's upper transit at meridian of Station 3245 ($17^h 14^m$, January 22, 1939, G.C.T.). Each dot marks a depth, length of vector from center gives amplitude (in meters) and its direction, the phase in lunar hours.

well, especially for the 12 hourly components where 10 of the 22 points lie inside.

Comparison of points on the diagrams do not suggest strong interrelationships of the properties of the two waves. Thus, for points lying inside the two ellipses, only those characterizing 6 isotherms were common to both and for those falling outside, only 3 were common to both, indicating that isotherms with large or small amplitudes in one wave do not necessarily have corresponding large or small amplitudes in the other. Thus, of the 6 isotherms with 12 lunar hour amplitudes in excess of 10 meters (18.0° , 17.5° , 17.0° , 16.0° , 15.0° , 14.0°) only one (18°) had a comparable 24 hour amplitude (13.33 meters); the others ranged from 1.57 to 5.41 meters. Likewise, the 6° isotherm with a relatively large 24 hour amplitude of 11.87 meters had a corresponding 12 hour amplitude of 8.24 meters only. Isotherms in the principal thermocline having smallest 24 hour amplitudes of 1.57 and 1.03 meters (14.0° and 13.0° isotherms) had

corresponding large 12 hour amplitudes of 11.82 and 5.78 meters, and isotherms of the smaller 12 hour amplitudes of 1.21 meters (7.5° and 8.0° isotherms) showed 24 hour amplitudes of 6.54 and 2.79 meters respectively.

Statistical constants for the lunar diurnal and lunar semidiurnal coefficients, as tabulated in Table 8, illustrate distinctions in geometric properties. Those tabulations under the heading "isotherms" were computed from harmonic constants derived from vertical oscillations of 22 isotherms (Table 4), whereas those under the heading "standard depths" are based on scaled phase and amplitude relations for forty-three 25 meter intervals, over a depth of 1050 meters. With regard to the use of scaled values, it was found that on comparison with a sufficient number of direct harmonic analyses at the depths concerned, satisfactory verification of the scaled coefficients was obtained and, as brought out by Table 8, geometric properties for the lunar diurnal and semidiurnal frequencies, whether based on coefficients derived directly from isothermal values or from scaled values for equal depth intervals, are without essential difference. Harmonic dials of interpolated values are given by Figs. 6 and 7 and, with the exception of the average properties, computations based on either set of point aggregates for a particular frequency may equally well characterize the water column to a depth of 1050 meters, this depth being the approximate lower limit of most significant stratification (Fig. 1).

TABLE 8

	Isotherms		Standard depths	
	12 ^h	24 ^h	12 ^h	24 ^h
σ_x	3.6024	4.3882	3.6103	4.3707
σ_y	5.9819	3.3949	5.7393	3.0349
r	-0.1043	0.16240	-0.18967	0.05292
M	6.983	5.548	6.7805	5.3211
P_1	7.0643	5.2591	6.8339	5.1528
P_2	4.2053	3.8749	4.1272	3.5638
P_1/P_2	1.6799	1.3572	1.6558	1.4459
θ	$95^\circ 35'$ (90°)	$16^\circ 01'$ (0°)	$100^\circ 47'$ (90°)	$4^\circ 02'$ (0°)
Av. Vector	—	—	4.38	2.21

Statistical constants computed for 50 per cent correlation ellipses from harmonic coefficients of lunar diurnal and lunar semidiurnal waves. Data under heading "isotherms" based on harmonic coefficients as computed for vertical oscillations of isotherms (in Table 4); data under heading "standard depths," based on harmonic coefficients for every 25 meters (0-1050 meters), scaled from those computed for isotherms.

For the semidiurnal coefficients, σ_y is significantly greater than σ_x , whereas for the diurnal, σ_x is greater than σ_y . Consequently, a marked ellipticity, most pronounced for the semidiurnal cloud, is an essential feature in both distributions. The directions of the major axes of the ellipses differ by 90° . Actual computation gives $\theta = 95^\circ 35'$ and $\theta = 100^\circ 47'$ for the semidiurnal coefficients and $\theta = 16^\circ 01'$ and $\theta = 4^\circ 2'$ for the diurnal, but, since rotation of the ellipse depends directly on the magnitude of the correlation coefficient, r (Table 8), which does not in either case differ significantly from zero (as shown below), the value of θ is taken to be 0° or 90° depending on whether σ_x or σ_y is the greater.

Testing the significance of r on the basis of the null hypothesis (assuming the correlation coefficient for an infinitely large supply of paired values following the normal law to be zero), the probability of any value of r arising because of random sampling errors, is with adequate accuracy given by the relative deviate k of r in the normal distribution of zero mean, referred to values of the normal probability integral.¹²

In a sample size of $N = 20$, or above, the standard deviation (σ_r) of the true distribution of r distributed normally about 0 is:

$$\sigma_r = \frac{1}{\sqrt{N-1}}$$

and the relative deviate k of r in the normal distribution of zero mean is:

$$k = \frac{r - 0}{\frac{1}{\sqrt{N-1}}} = r\sqrt{N-1}.$$

Thus for the 12 lunar hour wave:

r computed from harmonic coefficients of isotherms = -0.10432

$$k = 0.10432\sqrt{22-1} = 0.478,$$

and the probability of the deviate being exceeded is:

$$P = 0.631;$$

¹² When k is the relative deviate of the measure normally distributed, and P the probability of the k magnitude being exceeded solely through errors of random sampling, then:

$$P = \frac{\text{area of tail beyond } k}{\text{area of curve segment having same sign as } k}.$$

Values of P are rapidly obtained from a table of normal curve functions.

also, r computed from interpolated coefficients = -0.18967 ,

$$k = 0.18967\sqrt{43-1} = 1.229,$$

and the probability of the deviate being exceeded is:

$$P = 0.219.$$

For the 24 lunar hour wave:

r computed from harmonic coefficients of isotherms = 0.1624 ,

$$k = 0.1624\sqrt{22-1} = 0.744,$$

and the probability of the deviate being exceeded is:

$$P = 0.459;$$

also r computed from interpolated coefficients = 0.0529 ,

$$k = 0.0529\sqrt{43-1} = 0.343,$$

and the probability of the deviate being exceeded is:

$$P = 0.734.$$

Hence in all cases the correlation coefficients are of no apparent statistical significance, and the angle θ is not significantly different from 0° or 90° , depending on whether σ_x or σ_y is greater. The amount by which θ varies without consequence because of chance variation of r is estimated on the basis of a 5 per cent level being the demarcation point of significant deviations, in which case the limit of significant values of k will be just under 2 and correlation coefficients up to twice the standard deviations, σ_r , will be considered arising by chance.

For the case where $N = 22$, the standard deviation of r is:

$$\sigma_r = \frac{1}{\sqrt{N-1}} = 0.2182,$$

and when r is less than $2\sigma_r = \pm 0.4364$, θ will not differ significantly from 0° to 90° . In the computation of θ from the 12 lunar hour coefficients (isothermal values):

$$\frac{\sigma_x\sigma_y}{\sigma_x^2 - \sigma_y^2} = -0.94489,$$

which substituted together with the value of $2\sigma_r = -0.4364$ for r , in the equation:

$$\tan 2\theta = 2r \frac{\sigma_x\sigma_y}{\sigma_x^2 - \sigma_y^2} = 0.8730$$

gives a value of $20^{\circ} 35'$ as the latitude of chance variations in θ . Similarly for the 24 lunar hour coefficients (isothermal values):

$$\frac{\sigma_x \sigma_y}{\sigma_x^2 - \sigma_y^2} = 1.9271,$$

which substituted with the value of $2\sigma_r = 0.43649$ in the equation for θ gives $29^{\circ} 40'$ as the latitude of chance variation in θ .

In the Bartels' ¹³ approach to time series analysis, amplitude and phase of the average sine wave for each harmonic dial point aggregate are represented by an average vector, the end point of which is the mass center (Figs. 6 and 7). Of the several possibilities for testing reality of average vectors, one chosen by Bartels is to compare the observations (vectors plotted in harmonic dials) with the so-called random walk; ¹⁴ it being supposed that points plotted in the dials were chosen at random from a normally distributed aggregate. The expectancy, m , for the average amplitude, defined as the square root of the average square distance of the points is:

$$m = \sqrt{\frac{l_1^2 + l_2^2 + \dots + l_n^2}{n}} / \sqrt{n},$$

and the probability that the average vector, C , (vectorial sum divided by n) exceeds its expectancy in the ratio $k = C/m$ is:

$$P_{(k)} = e^{-k^2}.$$

$P_{(k)}$ is shown by Bartels to be exactly the probability that, under random walk conditions, an amplitude greater than $C = km$ should be found.

Thus, for the lunar diurnal coefficients, the average amplitude (C) of vertical displacements of the water column between 0 and 1050 meters, computed as the vectorial sum of 43 vectors, is 2.2058 meters. Under random conditions, the expectancy for the average amplitude of the 43 individual waves is:

$$m = \sqrt{\frac{1427.2735}{43}} / \sqrt{43} = 0.87859,$$

$$k = \frac{C}{m} = \frac{2.2058}{0.87859} = 2.5106$$

and

$$P_{(k)} = e^{-(2.5106)^2} = 0.00183.$$

¹³ Bartels, J. "Random Fluctuations, Persistence, etc." *Terrestrial Magnetism and Atmospheric Electricity*, XL, No. 1, pp. 1-60, 1935.

¹⁴ Originally formulated by Karl Pearson: "The Problem of the Random Walk." *Nature*, LXXII, p. 294, 1905.

Hence the probability for chance occurrence is once in about 500 trials, a value generally considered as not too small to make a definite claim that the observations do not correspond to the random walk with which they have been compared and an assumption of reality is warranted.

For the lunar semidiurnal coefficients, the average amplitude (C) of vertical displacements between 0 and 1050 meters, computed as before, is 4.383 meters. Under random conditions, the expectancy for the average amplitude of the 43 individual waves is:

$$m = \sqrt{\frac{2802.8508}{43}} / \sqrt{43} = 1.23121,$$

$$k = \frac{C}{m} = \frac{4.382}{1.2312} = 3.5594$$

and

$$P_{(k)} = e^{-(3.5594)^2} = 0.000000315.$$

The probability for chance occurrence is so small that, as in the previous case, reality of the semidiurnal average vector may be assumed (Figs. 6 and 7). Significance of the average vectors in relating Internal Wave and tidal phenomena is discussed later.

THE THEORETICAL INTERNAL WAVES

Additional consequences of the preceding statistical analysis are revealed by consideration of the theoretical Internal Waves contingent in the water masses under consideration. Thus, in a sea where density varies continuously with depth, possible wave motion is disclosed by investigation of the second order differential equation: ¹⁵

$$\frac{d^2 W}{dZ^2} + \lambda^2 g \varphi W = 0$$

with boundary conditions:

$$\begin{array}{lll} W = 0, & Z = 0, & \text{at the bottom} \\ W = 0, & Z = h, & \text{at the surface.} \end{array}$$

W represents the elevation of a water particle from its equilibrium position, φ is taken as $d\sigma/dZ$ (vertical variation of density), and $\lambda^2 g$, an unknown parameter, depends on density distribution. The integration is carried out numerically, and an infinite number of solutions, corresponding to an infinite number of Internal Waves are possible; values of W are relative and

¹⁵ Fjeldstad, Jonas Ekman. "Interne Wellen." *Geofysiske Publikasjoner*, X, No. 6, 35, pp., 1933.

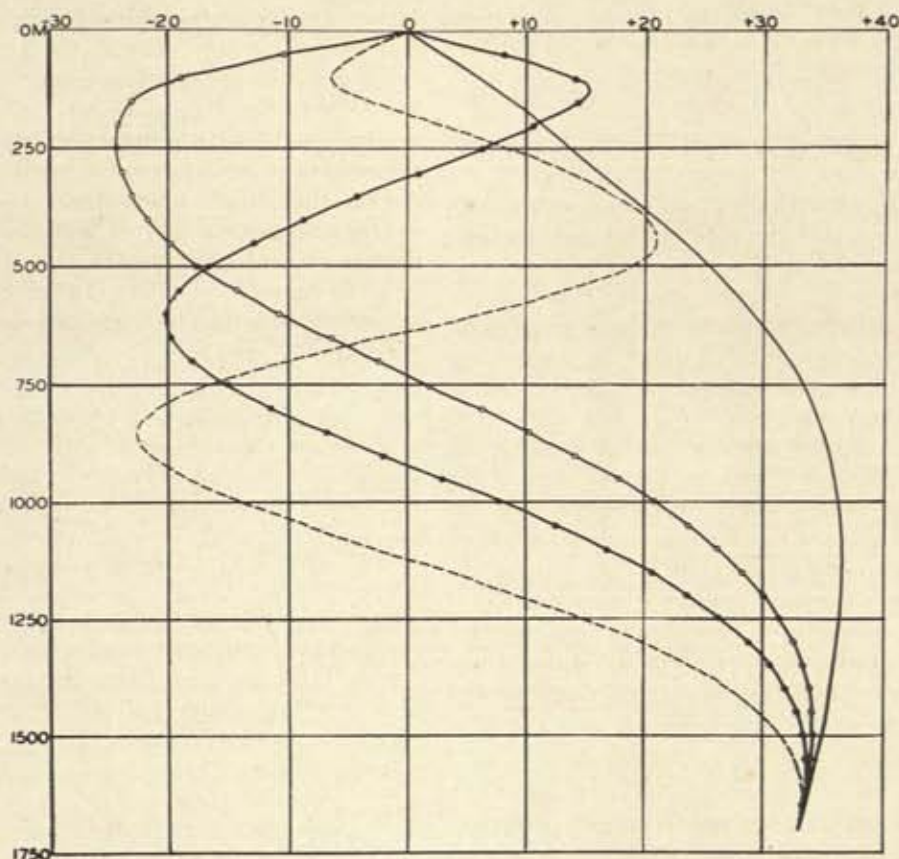


FIG. 8. Vertical distributions of first four Internal Waves; relative values, W , at "Atlantis" Station 3245.

distributions for the first four orders, between surface and 1700 meters are illustrated by Fig. 8. The first order wave is characterized by vertical displacements of the same phase with one maximum, the second order wave by two maxima of opposite phase, the third order wave by three maxima of opposite phase, and the fourth order wave by four maxima of opposite phase (Table 9). Horizontal velocity of the Internal Wave current is zero at the maximum of vertical displacement.

Absolute theoretical displacements of significant isotherms were determined by fitting W values (by least squares) to the diurnal and semi-diurnal coefficients of sine waves as computed directly from observed vertical displacements of 22 isotherms (Table 4). The theoretical lunar diurnal and semidiurnal coefficients, so obtained for vertical displacements of 20 isotherms at Station 3245 (identical with isotherms tabulated in Table 4 with the 7.0° and 6.0° omitted) and the fifty per cent probability ellipses fitting the

scatterings, are entered in harmonic dials (Fig. 9); statistical constants for these new distributions are tabulated in Table 10.

Before proceeding to examination of the new statistical results, the probability that computed values of the correlation coefficients, r , arise because of random sampling errors, and corrections for θ in the theoretical results are considered. Thus, for a sample, $N = 20$, the standard deviation, σ_r , of the true distribution of r distributed normally about 0 is:

$$\sigma_r = \frac{1}{\sqrt{N-1}} = \frac{1}{\sqrt{19}} = 0.2294.$$

For the theoretical 12 lunar hour point aggregate, the relative deviate k of r in the normal distribution of the zero mean is:

$$k = \frac{r - 0}{\frac{1}{\sqrt{N-1}}} = 3.609,$$

TABLE 9

Depth	1st order wave	2nd order wave	3rd order wave	4th order wave
0	0.00	0.00	0.00	0.00
100				-0.6405
120			1.5421	
170				0.0000
230		-2.4237		
310			0.0000	
430				2.1088
610			-2.0188	
640				0.0000
730		0.0000		
850				-2.2508
920			0.0000	
1120				0.0000
1130	3.6610			
1490		3.4183		
1570			3.3729	
1630				3.3370

Maxima and minima of relative displacement amplitudes, W , first four orders of Internal Waves, Station 3245.

the probability of the deviate being exceeded is:

$$P = 0.0003,$$

and the correlation coefficient is of apparent statistical significance. Chance variations in r of two times its standard deviation, σ_r , will produce variations in the computed value of θ . Thus letting:

$$r = 0.828 - 2\sigma_r$$

$$\tan 2\theta = \frac{2r\sigma_x\sigma_y}{\sigma_x^2 - \sigma_y^2} = -0.8673$$

$$\theta = 69^\circ 33',$$

equivalent to a possible increase of 11 degrees above the computed value (Table 10), but nearly 20 degrees less than θ characterizing the 12 hourly group of observed values (Table 8).

For the theoretical 24 lunar hour point aggregate the relative deviate k of r in the normal distribution of the zero mean is:

$$k = \frac{r - 0}{\frac{1}{\sqrt{N - 1}}} = 1.674,$$

and the probability of the deviate being exceeded is:

$$P = 0.0949.$$

Since the 5 per cent level is generally selected as the demarcation point of significant deviations, reality of the correlation coefficient is, in this

case, doubtful, and apparently the result of chance variations. Hence, the angle θ is zero (σ_x greater than σ_y), identical with θ for the observed 24 hour point aggregate.

Regardless of irregular interference of various influences, the statistical distinctions between theoretical 12 and 24 hour point aggregates are similar to those existing between the two groups of coefficients computed directly from observations (Tables 8 and 10). For the theoretical semidiurnal group, σ_y is greater than σ_x and for the 24 hour, σ_x exceeds σ_y ; likewise the absolute scattering of points, M , the major axis, P_1 , the ellipticity, P_1/P_2 , and the average vector of the semidiurnal group exceed the diurnal. The major axis of the theoretical diurnal ellipse is (like the observed) in a direction clockwise from the major axis of the semidiurnal ellipse (Figs. 4, 5, and 9); actual computation gives the direction as 1.96 lunar hours for the former and 13.06 lunar hours for the latter. However, since the correlation coefficient, r , for the diurnal point aggregate is not significantly different from 0, the major axis direction is taken as 12 hours, whereas for the semidiurnal group, chance variations of two times the standard deviation of r permits a major axis direction of 2.32 hours.

Comparison of theoretical and observed 12 hour coefficients shows, as a striking feature, an increased ellipticity of the former from $P_1/P_2 = 1.68$ to $P_1/P_2 = 3.61$ (major axis increased 53 per cent and minor axis diminished by 29 per cent), illustrating the theoretical semidiurnal wave motions of the water column to be of more nearly opposite phase with a corresponding smaller average amplitude (Tables 8 and 10). The absolute scattering of points, M , increased from 6.983 to 9.534 for the theoretical aggregate, and relative to the average amplitude the scatter-

TABLE 10

	Lunar semidiurnal	Lunar diurnal
σ_x	5.259	1.626
σ_y	7.953	0.908
r	0.828	0.348
M	9.534	1.860
P_1	10.8233	1.9732
P_2	3.0022	0.9583
P_1/P_2	3.6051	2.059
θ	58° 36'	15° 57'
	(69° 33')	(0°)
Av. Vector	2.604	1.38

Statistical constants computed from theoretical harmonic coefficients for vertical displacements of 20 isotherms (see text).

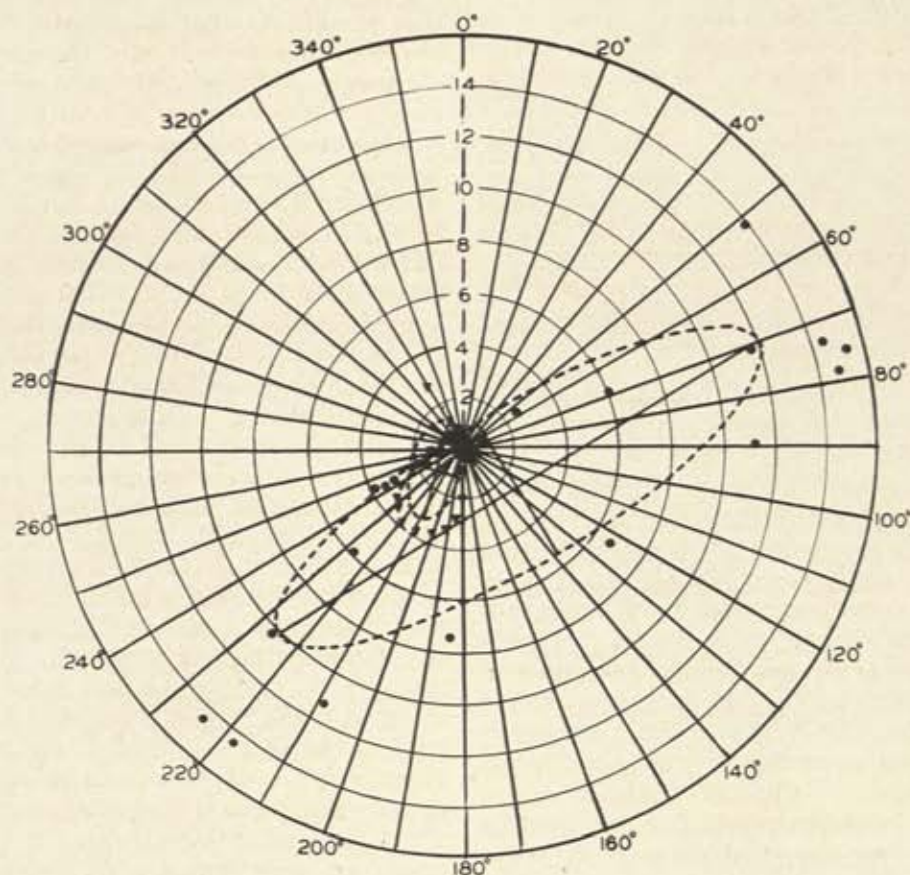


FIG. 9. Harmonic dials of theoretical semidiurnal, \odot , and diurnal, \triangle , vertical displacements of 20 isotherms computed from Fjeldstad's theory (see text). Scale references identical with those for dials of observed displacements (Figs. 4 to 7). Orientation of 50 per cent probability ellipses according to computed values of θ .

ing was 0.273 for the theoretical as compared with 0.514 for the observed point aggregate. The direction of the major axis of the theoretical ellipse with a possible value of 2.32 hours is not greatly different from the value of 3 hours computed for the major axis direction of the ellipse characterizing the observed coefficients.

Positions of the axes of the ellipses characterizing both groups of semidiurnal coefficients indicate greater variability among phase angles than amplitudes (Figs. 5 and 9). Thus, the major axis' end points for the theoretical 12 hour coefficients corresponded to amplitudes of 10.1 and 12.1 meters and to phase angles of 70° and 225° ; the minor axis' end points corresponded to 1.1 and 5.5 meters and 30° and 138° . Observed amplitudes are somewhat more variable than the theoretical; the major axis' end points corresponded to amplitudes of 3.6 and 10.7 meters and to phase angles of 93° and 261° , and the

minor axis' end points to 5.1 and 5.9 meters and 44° and 143° . Greater variability of observed amplitudes is to be expected since theoretical amplitudes, although in general larger, are more balanced by nearly opposite phase angles.

Comparison of the two groups of 24 hour coefficients (Tables 8 and 10) shows increased ellipticity for the theoretical point aggregate from $P_1/P_2 = 1.36$ to $P_1/P_2 = 2.06$, thus, indicating that theoretical diurnal wave motions were also balanced by more nearly opposite phases. The absolute scattering of the points, M , diminished from 5.55 for the observed to 1.86 for the theoretical group. Rotation of both ellipses appears to be identical, the directions of both major axes being taken as 12 hours.

Positions of the 24 hour ellipse axes indicate greater space variability of phase angles than of amplitudes (Figs. 4 and 9). The major axis' end points of the theoretical ellipse corresponded

to amplitudes of 1.2 and 3.2 meters and to phase angles of 210° and 334° , minor axis' end points corresponded to 1.2 and 2.2 meters and to 190° and 255° . Some increased variability characterizes the observed coefficients, the major axis' end points corresponding to amplitudes of 5.2 and 5.8 meters and to phase angles of 196° and 342° , and minor axis' end points to 2.4 and 5.6 meters and to 98° and 267° .

GEOPHYSICAL PROPERTIES OF THE VERTICAL OSCILLATIONS BROUGHT OUT BY ANALYSIS

The previous procedure of representing a set of ordinates over the interval $t = 0$ to $t = T$ as a sum of two sine waves is purely mathematical and does not involve the physical nature of the Internal Wave phenomenon described by the ordinates. In particular, the fact that the sum of the two sine waves is periodic, repeating values after intervals which are multiples of T , does not imply a similar property of this phenomenon outside the range of observation. Questions of the physical meaning of the extracted sine waves and of their average properties and space variabilities for the most part will remain unanswered until additional critical information, in forms suitable for comparison with analogous geophysical phenomena, is available. The technique used in analysis of the vertical oscillation time series was developed chiefly by J. Bartels¹⁶ for research on variability of diurnal variations in certain geophysical time series. However, unlike the long series analyzed by Bartels, the present interpretation of results of harmonic analyses of vertical displacements deals with space rather than with time variability. The statistical perspectives brought out by the analysis are basically important in characterizing distinctions in space distributions of lunar diurnal and semidiurnal vertical oscillations of the water column (for the observation period at Station 3245) and in indicating a connection between vertical oscillation and tidal mechanisms. The information in Table 8 is conducive to the comparison of Internal Wave effects throughout the ocean space.

Dissimilarities in the 24 and 12 lunar hour waves are clearly discernible. The harmonic coefficients of observed displacements, plotted in

the two harmonic dials, reveal that identical points did not have corresponding large or small amplitudes, and with the exception of a marked ellipticity, characteristic to both, geometric properties of the two point aggregates differed significantly (Figs. 4, 5, 6, 7, Table 8). The 12 hourly coefficients possessed most marked ellipticity, largest average amplitudes and greatest amounts of scattering. However, the pronounced ellipticity of both point aggregates indicates the small average amplitudes are produced by combinations of larger amplitudes but of nearly opposite phases. The phase of the average vector for the semidiurnal coefficients of observed displacements (between 0 and 1050 meters) was 2.97^h referred to Greenwich zero, or approximately 43 minutes before the upper culmination of the moon at the meridian of Station 3245, whereas that for the diurnal cloud was approximately 14 lunar hours later, 17.20 hours after Greenwich zero or $13^h 31^m$ after the local upper culmination. Further differences in space characteristics of the two waves are a variation in directions of major axes of the probability ellipses (03^h for the semidiurnal, 12^h for the diurnal) and by major axis direction of the semidiurnal cloud nearly coinciding with the phase of its average vector, whereas for the diurnal cloud the directions differed by more than 5 hours.

The properties of the average vectors suggest a connection between Internal Wave and tidal mechanisms. As illustrated by Table 8, average phases and amplitudes of the semidiurnal and diurnal coefficients (at 25 meter intervals) between surface and 1050 meters were:

Semidiurnal: 4.38 meters, 2.97^h (89°)

Diurnal: 2.21 meters, 17.17^h ($257^\circ 30'$):

And the phase difference (diurnal minus semidiurnal) of 2.2 lunar hours is not greatly different from the approximate 3.5 hour difference in phases of the semidiurnal and diurnal tides¹⁷ at the geographical position of Station 3245 as shown by cotidal charts of R. Sterneck¹⁸

¹⁷ Phase of semidiurnal tide scaled to be approximately 11.5 lunar hours and that of diurnal tide approximately 15 lunar hours.

¹⁸ Diurnal and semidiurnal cotidal charts of R. Sterneck reprinted by Albert Defant: "Die Gezeiten und Inneren Gezeitenwellen des Atlantischen Ozeans." *Deutsche Atlantische Expedition, "Meteor," 1925-1927, VII, Part 1, 1932, Fig. 197 (Page 283) and Fig. 203 (Page 292)*. See also R. Sterneck: "Die Gezeiten im Atlantischen Ozean," *Annalen der Hydrographie und Maritimen Meteorologie*,

¹⁶ Reference footnote 13. See also: Hafstad, L. R. "On the Bartels Technique for Time-Series Analysis, and its Relation to the Analysis of Variance." *Journal of the American Statistical Association*, 35, 347-361, 1940.

(Figs. 10 and 11). The relative importance of equilibrium heights of principal tidal components of the lunar tide¹⁹ as given by theoretical coefficients are:

M_2	N_2	S_2	K_1	O_1	P_1
0.4543	0.0880	0.2120	0.2655	0.1886	0.0880

And the equilibrium ratio,

$$\frac{M_2 + N_2 + S_2}{K_1 + O_1 + P_1} = 1.39,$$

is not greatly different from the ratio,

$$\frac{\text{semidiurnal}}{\text{diurnal}} = 1.982,$$

for average amplitudes of internal vertical displacements of the water column between 0 and 1050 meters at Station 3245.

Since tidal observations have been entirely restricted to the comparatively shallow portions of the sea actual conditions in the deep waters are unknown. The subject of ocean tides has not been accurately or completely treated and as a consequence, endeavors to link up tidal and Internal Wave mechanisms are made with caution. However, the intimation that the two mechanisms are associated appears to be further augmented by consideration of the ratio of amplitudes of the average semidiurnal and diurnal vectors (Table 8) in relation to available tidal information from the geographical locality of Station 3245.

As far as is known the tides in the ocean do not

48, No. 10, pp. 396-398, 1920, and "Die Gezeiten des Ozeans. 11. Sitzungsberichte der Akademie der Wissenschaften" in *Wien, Mathem.-Naturw. Klasse*, 130, 363-371, 1921.

¹⁹ Schureman, Paul. A manual of the Harmonic Analysis and Prediction of Tides. *Special Publication* No. 98, U. S. Coast and Geodetic Survey, 416 pp., 1924.

conform to the equilibrium theory,²⁰ and in the Atlantic Ocean, due to the smallness of the diurnal wave, the semidiurnal tide generally dominates. In low latitudes the ratio of $\frac{\text{semidiurnal}}{\text{diurnal}}$ tidal amplitudes frequently is considerably in excess of 2; along the eastern American coast it increases southward, for instance, from 2.92 at Wilmington, N. C., to 6.41 at Savannah, Ga., a location six and one half degrees north of Station 3245. Tidal information nearest to Station 3245 comes from the Caribbean region, where because the various basins respond in different degrees to the tide producing forces, the semidiurnal tides are very small and in places the total tide is largely diurnal. The ratios of semidiurnal to diurnal tide amplitudes of 2.98 to 0.25, computed from tidal harmonic constants (Table 11) for exposed West Indian Islands, include the average Internal Wave displacement ratio of 1.98 at Station 3245.

In the water column harmonic coefficients for vertical displacements of 22 isotherms reveal a trend which does not detract from the intimation of an association with tidal phenomena. In 19 cases occurrence of semidiurnal and diurnal maxima were within three hours of each other and in 14 of the 22 cases semidiurnal amplitudes dominated. As previously brought out, phase and amplitude changes are identified with the water column structure; greater vertical variations occurring in the more stratified parts. The dominance of the semidiurnal oscillation

²⁰ The equilibrium tidal theory requires a level ocean surface, a situation which cannot exist in nature because too great a length of time is required for the free wave to cross and recross.

²¹ Harris, Rollin A. Manual of Tides. Part IV A. Report of 1900, U. S. Coast and Geodetic Survey, Appendix No. 7, pp. 535-699, 1901.

²² Reference footnote 19.

TABLE 11

Place	Latitude North	Longitude West	M_2	S_2	N_2	K_1	O_1	P_1	$\frac{\text{Semidiurnal}}{\text{Diurnal}}$
Savannah, Tybee Is. Lgt.	32° 02'	80° 51'	3.22	0.59	0.68	0.34	0.24	0.12	6.414
Charleston, S. C.	32° 46'	79° 56'	2.48	0.43	0.56	0.34	0.25	0.11	4.957
Wilmington, N. C.	34° 14'	77° 57'	1.15	0.10	0.18	0.25	0.16	0.08	2.918
Port au Prince, Haiti	18° 34'	72° 22'	0.487	0.125	0.107	0.227	0.132	(0.082)	1.630
San Juan, Porto Rico	18° 29'	66° 07'	0.487	0.074	0.113	0.270	0.238	0.089	1.129
Culebra Island	18° 18'	65° 17'	0.293	0.043	0.048	0.250	0.186	(0.083)	0.740
St. Thomas Island	18° 20'	64° 56'	0.124	0.031		0.295	0.243	0.078	0.252
St. Lucia Island	14° 01'	61° 00'	0.246	0.127		(0.069)	0.056		2.980

Tidal Harmonic constants for selected stations nearest Station 3245, first three from Harris,²¹ last five from Schureman.²²

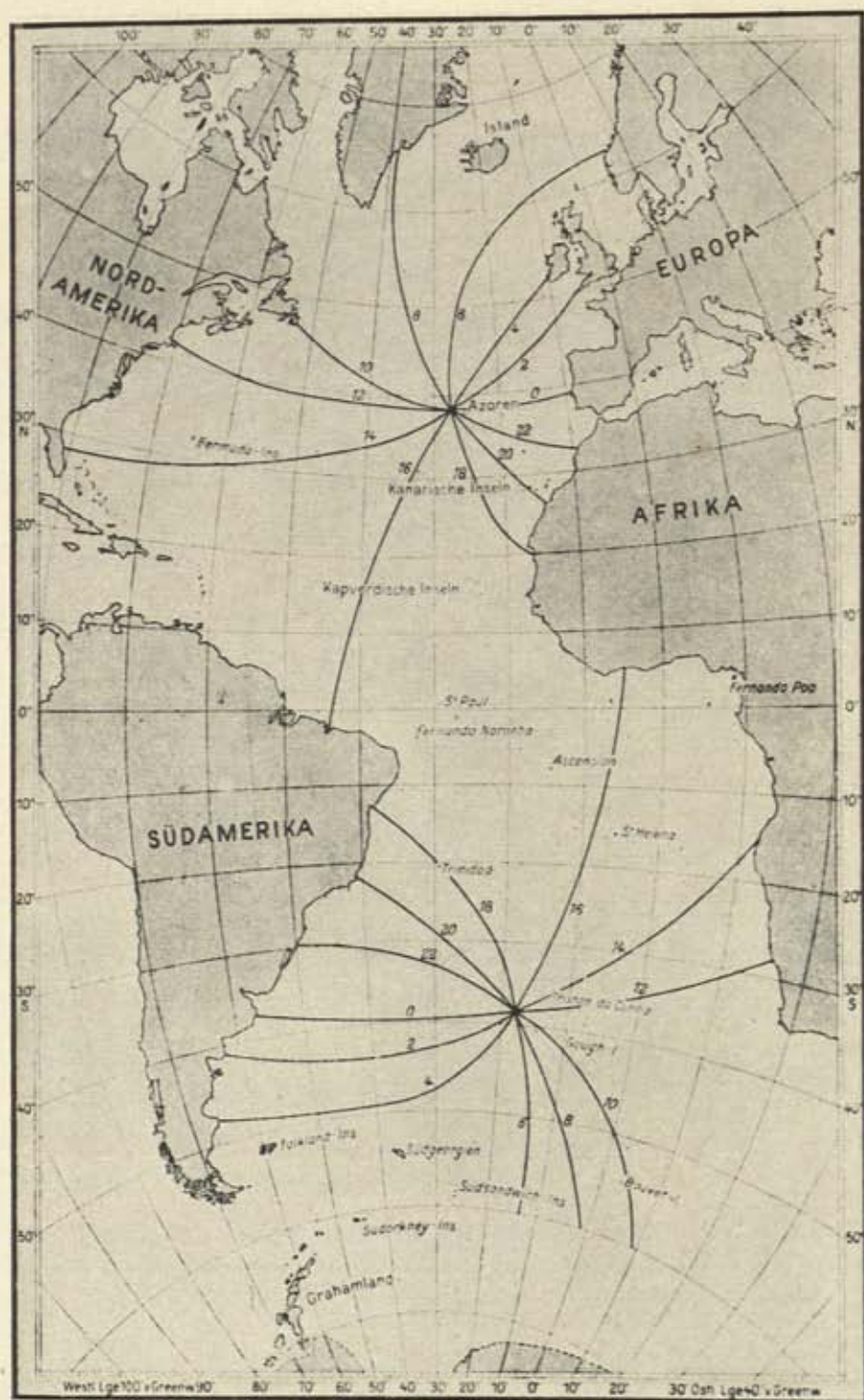


FIG. 11. Cotidal lines of diurnal tide in the Atlantic Ocean according to R. Sterneek (copied from Defant, see text).

in depths less than 700 meters (Table 4) becomes particularly striking in the more homogeneous water where maximum amplitude ratios $\left(\frac{\text{semidiurnal}}{\text{diurnal}}\right)$ reach 8.00. Still deeper (to 1050 meters), semidiurnal amplitudes diminished and the diurnal dominated, the minimum amplitude ratio $\left(\frac{\text{semidiurnal}}{\text{diurnal}}\right)$ being 0.185.

Throughout the water column the range of amplitude ratios was approximately equivalent to that recorded at shallow water tidal stations (Table 11) encircling Station 3245.

A general good agreement between phases of observed currents in the upper layers of the Atlantic (30° S to 30° N) and phases of the tide, as given by the cotidal maps of Sterneck (Fig. 10 and 11), has been brought out by Defant.²³ The results are of particular interest because the total currents measured at the "Meteor" anchor stations appear to be of mixed tidal and Internal Wave origin, in which case it seems likely that both were of the same, or nearly the same, phase. On the other hand, internal vertical displacements of the water layers are not necessarily in phase with the associated Internal Wave current. Examination of data from the eight "Meteor" anchor stations in the Atlantic reveals that (for identical stations) times of maximum displacements and of maximum current velocities differ by as much as 6 hours for the semidiurnal and by as much as 12 hours for the diurnal. Regularity between the two may be indicated by data from two "Meteor" stations (where observed currents and vertical displacements may appropriately be compared) on the high seas where (Table 12)

TABLE 12

"Meteor" station	Mean vertical displacement			Mean current			Phase difference	
	Depth	12h phase	24h phase	Depth	12h phase	24h phase	Displacement	Current
288	75-250	10.3 ^h	14.6 ^h	0-150	10.4 ^h	13.6 ^h	4.3 ^h	3.2 ^h
147	50-150	4.7 ^h	12.8 ^h	0-30	2.0 ^h	10.5 ^h	8.1 ^h	8.5 ^h

difference in phase between semidiurnal and diurnal vertical displacements (in approximately the same strata) was nearly equal to that be-

²³ Defant, Albert. "Die Gezeiten und Inneren Gezeitenwellen des Atlantischen Ozeans." *Deutsche Atlantische Expedition, "Meteor," 1925-1927*, VII, Part 1, 318 pp., 1932.

tween semidiurnal and diurnal currents. Information is too scanty for conclusions regarding general relationships between the phase of vertical displacements and the phase of current velocities throughout the ocean space, but the collective evidence strengthens the inference that the relationship between the average displacement vectors and tides at Station 3245 is not a chance result.

The Internal Wave theory of Fjeldstad has previously been tested by Fjeldstad²⁴ and Lek,²⁵ who using suitable observations from the Norwegian Fjords and from the waters of the Dutch Indies, respectively, obtained acceptable agreement between observed and theoretically computed results. The present investigation goes further in that the statistical treatments of results of the analytical transformations reveals the significant space characteristics of both observed and theoretical values to be closely identical. Complete agreement is not to be expected since at any time irregular influences (characteristic of all geophysical phenomena) may play a more or less important role, and in general support is given to the concept that observed vertical displacements are agreeably represented by the theoretical Internal Wave mechanism proposed by Fjeldstad.

Internal Wave propagation velocities, C_n , are computed from the parameter, λ , in the Fjeldstad equation, thus:

$$C_n = \frac{1}{\lambda_n} = \sqrt{\frac{g}{\lambda_n^2 g}}$$

Values of $\lambda^2 g$ used in the first four Internal Wave integrations at Station 3245 were:

1st order = 0.01458

2nd order = 0.08178

3rd order = 0.15299

4th order = 0.34200,

and the ensuing propagation velocities (Table 13) are compared with those at two other North Atlantic stations ("Michael Sars" No. 68, 39° 20' N, 50° 50' W, 5400 meters depth;²⁶ "Atlantis" No. 3091, 34° 02' N, 65° 54' W, 5100

²⁴ Fjeldstad, J. E. "Internal Waves." Communication at General Assembly of the International Association of Physical Oceanography, Edinburgh, September 1936. (Assoc. Oceanog. Phys., *Process-Verbaux*, No. 2, pp. 141, 142.) 1937.

²⁵ Lek, Lodewijk. "Die Ergebnisse der Strom- und Serienmessungen." *Report of the Snellius Expedition*, II, Part 3, 169 pp., 1938.

²⁶ Reference footnote 15.

meters depth²⁷) and at a South Pacific station ("Snellius" No. 253a; 01° 47.5' S, 126° 59.9' E, 1800 meters depth²⁸).

The first Internal Wave propagation velocity range of 42 cm sec. is reduced to 17 cm sec. for the three North Atlantic stations having depths in excess of 5000 meters. The lower velocity at "Snellius" Station 253a may reasonably be the result of its inferior depth of only 1800 meters. Ranges recorded for propagation velocities of Internal Waves above the second order (about 10 cm sec.⁻¹) are of doubtful significance

TABLE 13

Internal wave order	Station 3245	Station 3091	Station M.S.-68	Station S-253a
1	259	276	267	234
2	110	87	90	116
3	80	70	75	77
4	54	50	49	58

Velocities of propagation (cm sec.⁻¹) for first four Internal Waves computed for "Atlantis" Stations 3245 (25° 32' N, 53° 45' W) and 3091 (34° 02' N, 65° 54' W), "Michael Sars" Station 68 (39° 20' N, 50° 50' W), and "Snellius" Station 253a (01° 47.5' S, 126° 59.4' E).

in view of discrepancies entering into computation of the parameter $\lambda^2 g$.

The velocity diminution with increasing order, as brought out by Table 13, is an approximate harmonic progression, and from the weighted harmonic mean of the results fair approximation to the propagation velocities, C_n' , of Internal Waves in the open ocean is given by:

$$C_n' (\text{cms sec.}^{-1}) = \frac{221}{n}$$

Discrepancies in this empirical representation

²⁷ Reference footnote 3.

²⁸ Reference footnote 25.

chiefly affect the first two Internal Wave orders (+ 55 cm sec.⁻¹, 1st order; - 24 to + 5 cm sec.⁻¹, 2nd order); for higher orders, the differences appear irrelevant (± 6 cm sec.⁻¹).²⁹

The length of the lunar semidiurnal first order wave, L , having a propagation velocity of 221 cm sec.⁻¹ is:

$$L = 221 \times 12.45 \times 3600 = 99.05 \text{ km.}$$

Since the length of the semidiurnal tidal wave³⁰ is approximately 8800 km at a depth of 4000 meters (approximate mean depth of the oceans) the ratio of length of internal to tidal waves is in the vicinity of 1 to 100. Likewise the ratio of the mean depth of the oceans to length of the semidiurnal tidal wave is of the order of magnitude of 10^{-4} while that for the first Internal Wave is 10^{-2} .

APPENDIX 1

Temperature measurements at "Atlantis" Station 3245 (25° 32' N, 53° 45' W) between 02^h 54^m January 23 and 04^h 45^m January 24, 1939 (G.C.T.). Scaled values in each column based on samplings with 17 pairs of reversing thermometers; depths corrected from unprotected thermometer readings at 300, 800 and 1200 meter levels. Departures between computed observation depths and those measured by the hydrographic wire are given in Table 1. Sampling times are average for observations between the 100 and 1200 meter levels, maximum departure estimated not to exceed ± 3 minutes. Surface temperatures were taken separately and coincided with the 100 meter observation.

²⁹ The empirical equation gives 44 and 37 cm sec.⁻¹, respectively, for propagation velocities of 5th and 6th order Internal Waves as compared to 39 and 32 cm sec. computed from the parameter $\lambda^2 g$ at Station 3245.

³⁰ Defant, Albert. "Gezeitenprobleme des Meeres in Landnahe." *Probleme der Kosmischen Physik*, VI, Hamburg, 80 pp., 1925.



Depth	02 ^h 54 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23
0	23.65	23.65	23.80	23.80	23.85	23.95	23.90	23.90	23.90	23.90	23.90	23.90	24.05	24.25
100	21.90	21.52	22.20	21.93	22.09	22.18	22.47	22.07	22.37	22.42	22.05	22.28	21.59	21.67
150	19.48	19.20	19.28	19.17	19.27	19.40	19.60	18.83	19.15	19.35	19.05	19.50	19.05	19.10
200	18.30	18.24	18.31	18.20	18.10	18.13	18.19	18.10	18.11	18.04	18.02	18.15	18.08	18.09
300	17.42	17.67	17.71	17.62	17.48	17.47	17.46	17.46	17.37	17.37	17.43	17.47	17.41	17.50
400	16.50	16.73	16.77	16.57	16.45	16.48	16.39	16.44	16.34	16.34	16.47	16.68	16.49	16.65
500	14.74	15.29	15.31	15.01	15.07	14.86	14.89	14.83	14.79	14.80	14.74	15.00	14.97	15.11
600	12.89	13.24	13.46	13.18	13.27	13.11	13.15	13.06	12.99	13.20	12.83	13.26	13.11	13.33
700	11.14	11.16	11.30	11.08	11.30	11.17	11.19	11.12	11.10	11.26	10.67	11.04	10.85	10.91
800	9.02	9.26	9.21	9.25	9.17	8.88	8.93	9.01	9.03	8.98	8.64	9.04	9.00	9.07
900	7.63	7.69	7.73	7.75	7.71	7.65	7.68	7.80	7.77	7.75	7.68	7.80	7.76	7.82
1000	6.39	6.39	6.45	6.55	6.39	6.31	6.41	6.60	6.79	6.70	6.64	6.52	6.49	6.48
1100	5.71	5.75	5.75	5.70	5.70	5.69	5.68	5.79	5.87	5.81	5.84	5.82	5.76	5.79

Depth	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 23	00 ^h 00 ^m Jan. 24	00 ^h 00 ^m Jan. 24	00 ^h 00 ^m Jan. 24	04 ^h 54 ^m Jan. 24
0	24.25	24.20	24.20	24.15	24.10	24.10	24.10	24.10	24.10	24.10	24.10	24.10	24.00	23.90
100	22.35	22.14	21.74	22.05	21.90	22.15	21.60	22.20	22.04	21.93	21.75	21.16	21.75	21.44
150	19.46	19.46	19.10	19.06	19.02	19.28	19.18	19.18	19.40	21.08	19.12	19.10	19.15	19.11
200	18.19	18.25	18.00	17.98	18.00	18.14	18.10	17.98	18.13	18.11	18.17	18.07	18.10	18.04
300	17.56	17.58	17.55	17.35	17.40	17.39		17.38	17.39	17.39	17.45	17.45	17.45	17.45
400	16.69	16.67	16.55	16.32	16.38	16.37		16.40	16.43	16.53	16.53	16.54	16.61	16.64
500	15.06	15.00	14.99	14.87	14.90	14.85		14.90	14.91	14.83	14.87	14.85	15.10	15.05
600	13.39	13.28	13.14	13.20	13.10	13.13		13.06	13.10	13.05	12.95	13.03	13.20	12.95
700	11.02	11.11	11.01	11.08	10.98	10.98		11.03	10.91	11.05	10.94	10.73	10.99	10.90
800	9.13	9.30	9.22	9.15	9.08	9.20		9.15	9.18	9.21	9.16	9.00	9.01	9.00
900	7.88	7.77	7.74	7.70	7.69	7.70		7.68	7.68	7.68	7.58	7.61	7.56	7.68
1000	6.44	6.31	6.32	6.30	6.29	6.35		6.30	6.61	6.62	6.69	6.50	6.44	6.48
1100	5.74	5.75	5.76	5.73	5.66	5.69		5.70	5.73	5.69	5.68	5.63	5.63	5.74

PALEOCENE FAUNAS OF THE POLECAT BENCH FORMATION, PARK COUNTY, WYOMING

PART II. LIZARDS¹

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(Communicated by WILLIAM B. SCOTT)

ABSTRACT

Based principally upon the study of fragmentary specimens from the Polecat Bench formation the following Paleocene lizards are described: *Exostinus? rugosus*, new species; *Provaranosaurus acutus*, new genus and species; *Peltosaurus jepseni*, new species; *Oligodontosaurus wyomingensis*, new genus and species; and *Haplodontosaurus*, new genus. The distribution of all Paleocene reptiles known from formations in North America is charted.

INTRODUCTION

THE fossil lizard materials upon which this paper is based were collected by Princeton Scott Fund expeditions while exploring Paleocene mammal localities in Park County, Wyoming. Most of the specimens are from the Silver Coulee beds of the Polecat Bench formation, the geology of which has been fully discussed by Jepsen (1930, pp. 490-491; 1940, pp. 231-238) in Part I of this series of reports upon the faunas of the Polecat Bench formation.

It is perhaps needless to refer to the meager character of the materials, consisting chiefly of dentary and maxillary bones with teeth. Upon such scanty evidence little can be accomplished in determining their true affinities. It is believed, however, that sufficient diagnostic characters have been found to distinguish them, and that new materials can be identified with them, and thus through future discoveries it is anticipated that all will be eventually characterized and classified within the suborder.

This collection, belonging to the Princeton Geological Museum, was placed in my hands for study through the generosity of my friend, Dr. Glenn L. Jepsen, who informs me that the field work of collecting the specimens was supported by the Scott Fund and by a cooperative grant from the Geological Society of America and from the American Philosophical Society. The illus-

trations were prepared by Mr. Sydney Prentice and Mrs. A. W. Aul.

Family IGUANIDAE Bonaparte, 1840

Genus EXOSTINUS Cope, 1873

Exostinus is a genus of uncertain family reference, although it has been provisionally included in the Iguanidae for a number of years. During this time new discoveries have been favorable to this assignment but its certain relationship may still be regarded as obscure. *Exostinus* now includes three species, *E. serratus* Cope from the Oligocene (Brule), *E. lancensis* Gilmore from the Late Cretaceous (Lance), and *E. rugosus* herein described.

Exostinus? rugosus, new species. Figs. 1, 2

Type.—Princeton no. 14559, posterior half of right maxillary bearing five teeth.

Referred specimens.—Princeton no. 14640, parts of both maxillaries, both dentaries, jugal, and fragmentary skull and jaw parts.

Distribution.—Princeton Quarry, Sec. 21, T 57 N, R 100 W, Park County, Wyoming; Silver Coulee beds, Polecat Bench formation.



FIG. 1. Posterior half of right maxillary of *Exostinus? rugosus*. Type, Princeton Mus. no. 14559. External view. Five times natural size.

Discussion.—A small iguanid lizard is distinguished from other forms in this collection of Paleocene fossils by the character of the ornamentation on the external surface of the type

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maxillary, a series of small tubercular clusters that are without distinct arrangement, as shown in Fig. 1. The teeth on this specimen are pleurodont with subcylindric shafts. It is quite evident, although not too clearly shown by the present specimen, that the compressed crowns are bicuspid, consisting of a large posterior denticle with a smaller cusp in front. Shallow, longitudinal grooves on the external side of some of the teeth lead to the point of division between the denticles on the crown. These grooves are suggestive of somewhat similar conditions found on the tricuspid teeth of *Chamops segnis* from the Lance. In the latter, however, the grooves are more distinct and the longer ones are found on the inside of the teeth.

Princeton no. 14640, from the same quarry as the type, consists of parts of both maxillaries, both dentaries, jugal and a few fragmentary skull and jaw parts. None of the tooth bearing bones is completely preserved, hence the total number of teeth cannot be determined. One dentary shows evidence of 14 teeth but an unknown number are missing from the front of the series. Five teeth occupy a longitudinal space of 3 millimeters as in *Exostinus lancensis*. A scar on the outer posterior surface of the dentary indicates the extent of the anterior process of the coronoid as being to a point below the second tooth from the posterior end of the series, as in most Iguanidae. Bicuspid teeth are present in both upper and lower dental series. There are a few crowns, however, on which this bicuspid condition cannot be detected.

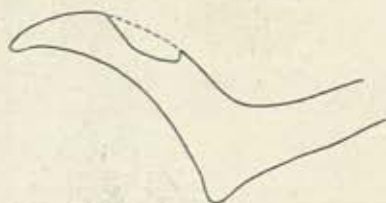


FIG. 2. Right jugal of *Exostinus? rugosus*. Princeton Mus. no. 14640. Lateral view. Five times natural size.

The jugal has the usual curved shape (Fig. 2) with a bluntly pointed triangular spur projecting backward from the posterior angle where the bone bends upward to form the posterior boundary of the orbit. The lower, outer surface of this bone is sparsely sculptured by a few short raised ridges that form an indefinite pattern. The type of sculpturing has a distinct resemblance to that found on the maxillary. This style of sculpturing on the jugal also distinguishes

this species from *Exostinus serratus* Cope, which has the jugal covered with flat, quadrangular bony tubercles.

On the basis of the sculpturing of the maxillary and the jugal as in *Exostinus serratus* this specimen is provisionally referred to a species of the genus *Exostinus*. From the other species of the genus, *E. serratus* Cope and *E.? lancensis* Gilmore, the present form is distinguished at once by the bicuspid maxillary and dentary teeth as contrasted with the simple crowns in both of those species. The specific name *rugosus* is, therefore, proposed for its reception. The species name was suggested by the rugose sculpturing on the maxillary and jugal surfaces.

Family VARANIDAE Bonaparte, 1831

Dollo, in 1923, described a varanid lizard, *Saniwa orsmaelensis* from the Orsmael and Erquelinnes localities of Belgium. At that time he believed that the late Landenian (Sparnacian) faunas were of Paleocene age, but the close similarity of the Sparnacian and the early Wasatchian mammals and other considerations now lead to the belief that most if not all of the deposits at Orsmael and Erquelinnes should be assigned to the Eocene. As Simpson (1929) states, however, "... the fauna of Orsmael retains some special affinity with the Paleocene. . . ."

At any rate the Silver Coulee beds are older than the Wasatchian sediments of the Bighorn Basin, as demonstrated by stratigraphic position, and hence are probably older than the deposits yielding *Saniwa orsmaelensis*.

Provaranosaurus acutus, new genus and species

Type.—Princeton Mus. no. 14243, left maxillary bearing 11 teeth.

Distribution.—Princeton Quarry, Sec. 21, T 57 N, R 100 W, Park County, Wyoming; Silver Coulee beds, Polecat Bench formation.

Discussion.—The maxillary selected as the type has been prepared in relief on a small block of matrix and thus only the external side is accessible for study. Fortunately the most anterior tooth was sufficiently exposed on the inner side to show the pleurodont character of its attachment. The dentigerous portion of the maxillary which has both ends completely preserved has an overall length of 23 millimeters. There are 11 teeth present in the jaw, but it is quite evident that several are missing from the complete series, as shown in Fig. 3.

The teeth are pleurodont, widely spaced, (in

contrast to the lack of diastemata in *S. orsmae-lensis*), have slender crowns, and are round in cross section, with sharply pointed tips. All of the longer teeth are inclined backward, but none

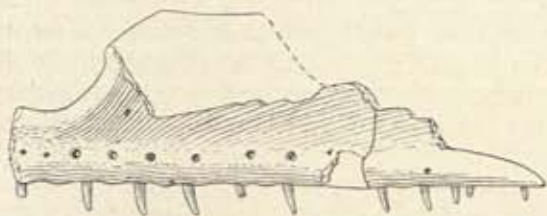


FIG. 3. Left maxillary of *Provaranosaurus acutus*. Type. Princeton Mus. no. 14243. Viewed from the left side. Three times natural size.

has the backward curvature found in the teeth of *Palaeovaranus* from the Phosphorites of France. The largest teeth are borne on the anterior half of the maxillary, and they gradually reduce in size posteriorly.

The anterior portion of a left dentary, Princeton Mus. no. 14561 is provisionally identified as pertaining to this same genus and species. The slender, sharp, simple crowned, widely spaced teeth, combined with the slenderness of the dentary as a whole all point to the correctness of such a conclusion. Toward the anterior end the dentary bends inward toward the symphyseal contact. On the lower internal side the bone is deeply furrowed by Meckel's groove which runs to the symphysis. On the median external side is the usual row of foramina. The teeth are pleurodont with expanded bases as in varanids generally, but they lack the basal striations found in *Varanus*, *Saniwa* and *Parasaniwa*.

Method of implantation, shape, and wide spacing of the teeth are all features indicating varanid affinities and this genus is therefore tentatively referred to the family Varanidae. If correctly assigned it is a representative of the family that occupies an intermediate position geologically between the Late Cretaceous (Lance) *Parasaniwa* and the Eocene (Bridger) *Saniwa*. The straight, slender, sharply pointed teeth without basal striations distinguish *Provaranosaurus* from the other members of the family.

Family ANGUIDAE Bonaparte, 1831

Genus PELTOSAURUS Cope, 1873

Peltosaurus jepseni, new species.

Figs. 4, 5, 6, 7, 8

Type.—Princeton Mus. no. 14565, incomplete right maxillary bearing 9 teeth, posterior portion of the parietal, and one dermal scute.

Paratype.—Princeton Mus. no. 13371, left maxillary bearing 13 teeth.

Distribution.—Type specimens from Princeton Quarry, Sec. 21, T 57 N, R 100 W, Park County, Wyoming, Silver Coulee beds, Polecat Bench formation. Additional specimens from this site; also from the Rock Bench quarry beds, Park County, Wyoming; from the Lebo of the Crazy Mountain field, Montana; and from the Dragon formation, Emery County, Utah.

Discussion.—The present species is based on a study of twenty-three specimens, six in the National Museum and seventeen in the Princeton Museum collections, of which Princeton Mus. no. 14565 is selected as a type. This specimen is of interest as furnishing the first available information on the character of the scutellation of these Paleocene lizards. The close resemblances found in the dentition, scutellation of head and body to the corresponding parts of those of *Peltosaurus granulosus* Cope confirms the correctness of the original assignment of some of the National Museum specimens to the genus *Peltosaurus* on meager materials (Gilmore 1928, p. 137).

The parietal consists of the posterior half with the right posterior process, the left is entirely missing. The superior surface is plane and except for a wide smooth band posteriorly is covered by bony scutes that are fully coalesced to the underlying bone. As shown in Fig. 4, the

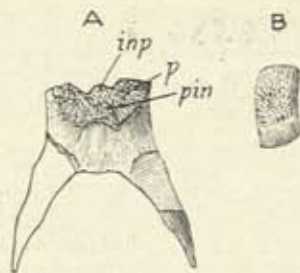


FIG. 4. Parietal and dermal scute of *Peltosaurus jepseni*. Type. Princeton Mus. no. 14565. A, posterior portion of parietal; B, dermal scute; inp, interparietal scute; p, parietal scute; pin, postinterparietal scute. Both figures three times natural size.

scutal area consists of two large parietal scutes that are separated on the midline by the interposition of a narrow interparietal. The latter is joined posteriorly by a small subtriangular postinterparietal. The arrangement of these scutes, insofar as they can be judged in their incomplete state, are in close agreement with those of *P. granulosus*, differing only in size,

proportions, and the style of ornamentation of their dorsal surfaces. *P. granulosus* has a granular sculpture of both head and body scutes, whereas in the present specimen, more especially the parietal scutes, are ornamented by a series of low radiating ridges with narrow intervening valleys. These ridges do not form a distinct pattern although the more conspicuous of the ridges have a decided trend backward and outward from the center of the scute as shown in Fig. 4. The posterior median border of the parietal between the divergent posterior processes is broadly hollowed out, as contrasted with the deep U-shaped notch in *P. granulosus*.

The dermal body scute, see Fig. 4-B, has the usual quadrangular shape with a narrow smooth, articular band across the anterior end. The remaining dorsal surface has a sculpture resembling that of the skull scutes, but with the pattern less well defined.

The type maxillary which bears nine teeth is slightly incomplete at both ends. In size, outline, and surface marking it is in complete accord with the more perfect paratype, Princeton Mus. no. 13371, on which the description to follow is based.

There are 13 teeth present in the paratype, but as shown in Fig. 5, it is clearly evident that two



FIG. 5. Left maxillary of *Peltosaurus jepseni*. Paratype. Princeton Mus. no. 13371. External view. Three times natural size.

are missing, thus 15 teeth would constitute the complete maxillary series, one tooth less than in *P. granulosus* which has 16 to 17, or *Melanosaurus* which has 16. The teeth are pleurodont, stout, shafts compressed fore and aft with flattened sides, and closely spaced in the jaw. The crowns are bluntly wedge-shaped with the longer bevel internal. On some of the crowns there is faint evidence of striae running downward at right angles to the cutting edge, but this sculpturing soon disappears with wear. The largest teeth are in the center of the series but they diminish both in size and length toward the ends of the maxillary. Upper teeth appear indistinguishable from the lower.

Over all the maxillary has a greatest length of

15.3 millimeters and the 15 teeth occupy a space of 13 millimeters.

Viewed laterally (see Fig. 5) the maxillary presents a narrow smooth surface paralleling the dentigerous border which is perforated by the usual row of foramina. Above this smooth area on the anterior half the surface is slightly roughened. A similar surface on the maxillary of *P. granulosus* marks the attachment of the lowermost of the dermal scutes which form such a conspicuous feature of the skull in that species.

In an earlier paper, an incomplete right maxillary bearing 8 teeth, U. S. N. M. no. 10920 was assigned to the genus *Peltosaurus*, (Gilmore 1938, p. 22) but without specific designation. In view of its close resemblance both in size and other characteristics it can now be definitely identified as pertaining to the present species. This specimen which comes from the Lebo (Fort Union No. 2) Paleocene, Sweetgrass County, Montana, considerably extends the known geographical range of the present species.

The lower jaw of *P. jepseni* is represented by several fragments of rami from the same locality and geological horizon as the type and paratype. Also in the Princeton Mus. collections are three specimens, nos. 14577, 14578, and 14579, from a lower level, the Rock Bench quarry beds, pertaining to this form. In the National Museum collections there are three incomplete dentaries, nos. 10444, 10446, and 10811, from the Lebo (Fort Union No. 2) of Sweetgrass County, Montana, that can also be referred to this genus and species.

One of the Silver Coulee specimens, a nearly complete right dentary, Princeton Mus. no. 14245 (Fig. 6) shows the complete dental series

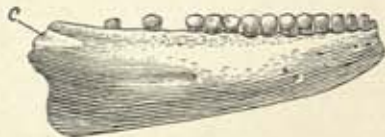


FIG. 6. Right dentary of *Peltosaurus jepseni*. Princeton Mus. no. 14245. Outer view. C, coronoid scar. Three times natural size.

to consist of not less than 17 teeth as contrasted with 21 in *P. granulosus*. These teeth occupy a space 12.3 millimeters in length. A scar on the upper posterior surface of the outside of the dentary indicates the point of overlap of the outer anterior process of the coronoid. Beneath it is the scar for the overlap of the broadly

rounded end of the surangular. The portion of a jaw illustrated in Fig. 7 shows the coronoid to sit astride the dentary as in *P. granulosus* with its tapering inner prolongation terminating opposite next to the last tooth. The splenial is the usual thin bone that covers Meckel's groove. Its ventral contact cannot be traced and the anterior end is missing. The splenial is perforated near its middle by a longitudinally elongated foramen.

The relatively longer and more closely spaced teeth as compared with those of *P. piger* are clearly indicated in Fig. 7.

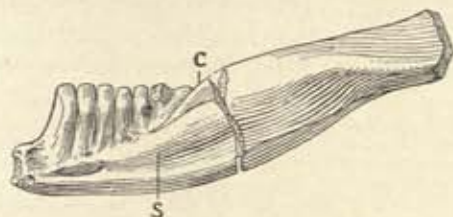


FIG. 7. Portion of a right ramus of *Peltosaurus jepseni*. Princeton Mus. no. 14244. Viewed from the inner side. C, coronoid; S, splenial. Doubtful contact at the median break. Three times natural size.

Two dentary fragments containing teeth, U. S. N. M. Nos. 16579 and 16583 from the Dragon formation, Paleocene, in the Manti National Forest, Emery County, Utah, are provisionally identified as pertaining to the present genus and species. These teeth are in perfect agreement with those described from the Paleocene of northern localities, both as to size and other characteristics.

A single thoracic vertebra, preserved in a small block of matrix in close proximity to a considerable number of dermal scutes of the *Peltosaurus jepseni* type, is provisionally identified as pertaining to that genus and species. If correct in this assumption it furnishes the first information had of the vertebral column. Only the ventral side is available for study at this time (see Fig. 8). The centrum is tapering, having a closer resemblance to the vertebra of *Iguana* than to the



FIG. 8. Thoracic vertebra of *Peltosaurus jepseni*. Princeton Mus. no. 14641. Ventral view. Five times natural size.

more quadrangular centra of *Peltosaurus granulosus*. The median, flattened ventral surface is defined by shallow longitudinal grooves on either side. The centrum as a whole is depressed, the cup and ball are transversely ovate, the latter set off by a shallow annular groove on the ventral side. The diapophyses project outward from the anterior lateral angles of the centrum but do not extend below its ventral border. The centrum has a greatest length of 4 mm., and a greatest width across the diapophyses of 3.2 mm.

The genus *Peltosaurus* now contains the following species, *P. granulosus*, *P. abbotti* both from the Oligocene, and *P. piger* from the Lance formation. *Peltosaurus jepseni* may be distinguished from the Oligocene species by its slightly smaller size and differences in the sculpture of the dermal scutes of head and body as previously described. The parietal also displays a broad, shallow notch on its posterior median border as contrasted with the deep U-shaped notch in *P. granulosus*. There also appear to be fewer teeth but due to the paucity of materials this observation needs verification.

From *P. piger*, the present species may be distinguished by the more slender form of its teeth, and by the greater length of their protrusion beyond the alveolar borders.

This species is named for Dr. Glenn L. Jepsen in appreciation of his outstanding contributions to our knowledge of the mammalian faunas from this same Wyoming area.

SAURIA OF UNKNOWN FAMILY REFERENCE

Oligodontosaurus wyomingensis, new genus and species. Fig. 9

Type.—Princeton Mus. no. 14246, consists of a left ramus bearing a complete dentition.

Distribution.—Princeton Quarry, Sec. 21, T 57 N, R 100 W, Park County, Wyoming, Silver Coulee beds, Polecat Bench formation.

Discussion.—This species is based on a left ramus that lacks its articular end posterior to the coronoid process. As preserved the ramus has a greatest length from end to end of 6.8 millimeters. The specimen has been relieved on a small block of matrix and thus only the internal side is available for study at this time. The complete dental series consists of 9 homodont teeth, all present except the crown of the most anterior one.

These are subpleurodont in manner of attachment and the 9 teeth occupy a longitudinal space

of 4.8 millimeters. The teeth are transversely compressed with lance-shaped crowns. The last tooth is the most robust of the series; the other teeth reduce in size anteriorly. The most an-

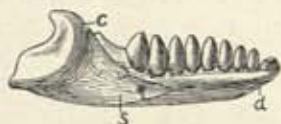


FIG. 9. Left ramus of *Oligodontosaurus wyomingensis*. Type. Princeton Mus. no. 14246. Internal view. C, coronoid; d, dentary; s, splenial. Five times natural size.

terior tooth situated on the very tip of the dentary has an enlarged base. The inclined shelf to which the teeth are attached is relatively narrow, occupying less than one half the total depth of the dentary. With the exception of there being fewer teeth in the series, their configuration and method of attachment have their closest resemblance in *Lanceosaurus hatcheri* from the Lance formation (Gilmore, 1928, p. 160, Fig. 104, p. 26, Fig. 8).

The coronoid is relatively stout, with truncated upper extremity, and strengthened on the inner side by a low, rounded ridge that originates well toward the top and extends downward with a decided backward curve on the lower half of the ramus where it merges with the prearticular. The inner anterior process of the coronoid that laps the dentary ends on the line of the posterior border of the last tooth.

The splenial appears to be very short, apparently terminating posterior to the mid length of the dentary as shown in Fig. 9. None of the other structural details of the posterior portion of the jaw can be certainly determined.

The diminutive size of the type coupled with the reduced number of teeth in the dentary with an enlarged posterior tooth and a reduced splenial constitute a series of characters sufficient to distinguish fully this genus and species from all known Sauria. At this time no clue has been obtained as to its proper family assignment.

Haplodontosaurus, new genus

Genotype, *Harpagosaurus excedens* Gilmore, Mem. Nat. Acad. Sci., vol. 22, No. 3, p. 157, Fig. 99, 1928.

The new genus *Haplodontosaurus* is proposed for the reception of the species *excedens*. Originally this species was provisionally referred to the genus *Harpagosaurus*. Its removal is brought about by a re-examination of the type in connec-

tion with the study of a complete maxillary (Princeton Mus. no. 14560) the dentition of which displays such close resemblances to the teeth of the type of *H. excedens* as to suggest their specific identity. If this conclusion is correct it permits comparison to be made with the type of *Harpagosaurus parvus* based on a maxillary from the Lance formation. This specimen (see Fig. 11) has a series of acutely pointed



FIG. 10. Right dentary of *Haplodontosaurus excedens*. Type. U. S. N. M. no. 10447. Lateral view. Five times natural size. After Gilmore.



FIG. 11. Right maxillary of *Harpagosaurus parvus* Gilmore. Type. U. S. N. M. no. 10803. Lateral view. About five times natural size. After Gilmore.

pleurodont teeth with cylindrical shafts and a long narial border that is moderately inclined to the horizontal; in *Haplodontosaurus excedens* the pleurodont teeth are bluntly pointed with shafts slightly flattened fore and aft, and the narial border is short and steeply inclined (see Fig. 12) indicating a high blunt muzzle as contrasted with the more attenuated nose in *Harpagosaurus parvus*. Mention should be made that this re-study of the type of *excedens* discloses it to be a dentary, not maxillary, as originally identified. This is indicated by the convex outer surface of the bone and the presence of a small portion of Meckel's groove.

HAPLODONTOSAURUS EXCEDENS (Gilmore, 1928)

In the Princeton lizard collection there are four specimens (nos. 14560, 14563, 14567 and 14569) identified as pertaining to the present genus and species. All are from the Silver Coulee beds,



FIG. 12. Right maxillary of *Haplodontosaurus excedens*. Princeton Mus. no. 14560. Lateral view. * Five times natural size.

Polecat Bench formation, Paleocene, and all were found in the Princeton Quarry, Sec. 21, T 57 N, R 100 W, Park County, Wyoming.

The most perfect specimen, a complete maxillary illustrated in Fig. 12, has a greatest length over all of 8 millimeters. There are 12 teeth preserved in the maxillary but it is clearly evident that the full complement would consist of 17 teeth. This fact furnished a further distinction between the two genera, as the maxillary of *Harpagosaurus parvus* carries only 14 teeth. The form of the maxillary is clearly depicted in Fig. 12 and thus requires no further description.

Specimen Princeton Mus. no. 14563 is a right maxillary lacking its anterior end. In size and all other characteristics it is in complete accord with the maxillary illustrated in Fig. 12.

The third specimen, Princeton Mus. no. 14567, is a small section of a left dentary bearing 4 teeth. These teeth have the fore and aft sides of the

shafts slightly flattened as in the type of the species. The crowns are more acutely pointed than those of the available maxillae. The fourth specimen, Princeton Mus. no. 14569, consists of the anterior end of a left maxillary carrying 6 or more teeth. It contributes no additional information concerning the species.

SUMMARY

Most of the Paleocene lizard specimens described herein were collected from one locality designated "Princeton Quarry" and located in Sec. 21, T 57 N, R 100 W, on the east side of Sand Coulee basin, Park County, Wyoming. This quarry has produced several hundred mammalian specimens, including a complete skeleton, a number of articulated skulls and jaws, vertebral columns, and limbs. Among the mammals Jepsen (1940, p. 236) has recognized

KNOWN DISTRIBUTION OF NORTH AMERICAN PALEOCENE REPTILES

	Mantua (Wyo.)	Puerto (N. Mex.)	Dragon (Utah)	Torrejon (N. Mex.)	Rock Bench (Wyo.)	Lebo (Mont.)	Ravenscrag (Sask.)	Paskapoo (Alberta)	Melville (Mont.)	Silver Coulee (Wyo.)	Bear Creek (Mont.)	Clark Fork (Wyo.)
Sauria												
Iguanidae												
<i>Exostinus? rugosus</i>										X		
Varanidae												
<i>Provaranosaurus acutus</i>										X		
Anguidae												
<i>Peltosaurus jepseni</i>			X		X	X				X		
<i>P. sp.</i>				X								
Family reference uncertain												
<i>Oligodontosaurus wyomingensis</i>										X		
<i>Haplodontosaurus excedens</i>						X				X		
<i>Machaeosaurus torrejonensis</i>				X								
<i>Harpagosaurus? silberlingi</i>						X						
Serpentes												
<i>Helagras prisciformis</i>		X		X								
Crocodylia												
<i>Leidyosuchus multidentatus</i>				X								
<i>Allognathosuchus mooki</i>		X										
Allognathosuchids undesc.....					X							X
Crocodylids undesc.....	X									X		
Rhynchocephalia												
<i>Champsosaurus puercensis</i>				X								
<i>C. saponensis</i>		X		X								
<i>C. australis</i>		X										
Champsosaurids undesc.....	X				X	X	X		X	X	X	X

KNOWN DISTRIBUTION OF NORTH AMERICAN PALEOCENE REPTILES—Continued

	Mantua (Wyo.)	Puerco (N. Mex.)	Dragon (Utah)	Torrejon (N. Mex.)	Rock Bench (Wyo.)	Lebo (Mont.)	Ravenscrag (Sask.)	Paskapoo (Alberta)	Melville (Mont.)	Silver Coulee (Wyo.)	Bear Creek (Mont.)	Clark Fork (Wyo.)
Chelonia												
Pleurosternidae												
<i>Compsemys parvus</i>		x		x								
<i>C. vafer</i>		x										
<i>C. puericensis</i>		x										
<i>C. torrejonensis</i>				x								
Baenidae												
<i>Baena escavada</i>				x								
<i>B. sp.</i>		x		x								
Dermatemydidae												
<i>Adocus hesperius</i>		x										
<i>A. substrictus</i>				x								
<i>A. onerosus</i>				x								
<i>A. annexus</i>				x								
<i>Hoplochelys crassa</i>		x										
<i>H. bicarinata</i>		x										
<i>H. laqueata</i>		x										
<i>H. saliens</i>				x								
<i>H. paludosa</i>				x								
<i>H. elongata</i>				x								
<i>H. caelata</i>						x						
Plastomenidae												
<i>Plastomenus acupictus</i>				x								
<i>P. torrejonensis</i>				x								
<i>P. sp.</i>		x		x								
Emydidae												
<i>Clemmys backmani</i>							x					
Trionychidae												
<i>Aspideretes sagatus</i>		x										
<i>A. puericensis</i>		x										
<i>A. reesidei</i>		x										
<i>A. vegetus</i>		x										
<i>A. quadratus</i>		x										
<i>A. perplexus</i>		x										
<i>A. singularis</i>				x								
<i>A. superstes</i>								x				
<i>A. cf. subquadratus</i>							x					
<i>A? nassau</i>									x			
<i>A. sp.</i>				x								
<i>Conchochelys admirabilis</i>		x										
<i>Amyda eloisae</i>		x										
<i>Platypeltis antiqua</i>				x								
Chelonids undesc.	x		x		x			x		x	x	x

nine orders, seventeen families, and twenty-eight genera, and states that there are others, as yet unstudied, mammalian forms represented. The quarry has yielded also at least two kinds of amphibia, one represented by a complete skull and jaws and part of the vertebral column. These will be described in another part of this series of publications upon the faunas of the Polecat Bench formation.

In addition to the three families and five genera and species described herein, there are only two other species of Paleocene lizards known from the United States. These are *Harpagosaurus? silberlingi* from the Lebo of Montana (Gilmore 1938, pp. 24-25), and *Machaeosaurus torrejonensis* from the Torrejon of New Mexico (Gilmore, 1928, pp. 155-156). That there were other as yet undescribed members of the Sauria in the

Paleocene is indicated by fragmentary specimens in both the Princeton and the United States National Museum collections but these materials are too meager for characterization.

In the belief that a tabulation of the reptilia known from the Paleocene of North America will be useful, the following chart is presented to summarize the geological distribution of the various forms:

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STUDIES OF LIVING NERVES. VIII. HISTORIES OF NERVE ENDINGS IN FROG TADPOLES SUBJECTED TO VARIOUS INJURIOUS TREATMENTS¹

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CONTENTS

Abstract	168
Introduction	168
Complete degeneration of nerve endings of terminal arborizations	170
Histories of nerve endings in tadpoles subjected to electric shocks	170
Histories of nerve endings in starved tadpoles	172
Histories of nerve endings in or near regenerating zones	174
Histories of nerve endings under various other conditions	175
Ciné-photomicrographic records of nerve ending histories	177
Comments	181
Summary	181

ABSTRACT

Case histories are presented of individual nerve endings of terminal arborizations of myelinated fibers in frog tadpoles subjected to various kinds of injurious treatments. Electric shocks, starvation, chloretone anesthesia, wound infliction, insulin, and heat have each been used to induce nerve ending irritation. Swelling, retraction, and variable amounts of degeneration characterize markedly irritated endings. Reduction of swelling, extension, and branching characterize endings in process of recovery. Changes associated with chronic neuritis, such as are induced by starvation, are essentially similar to those associated with acute neuritis, such as are induced by electrical injury.

Examples are also presented of the behavior of rapidly growing nerve tips in young regenerating zones, as these are subjected to acute irritative treatments of several kinds. In regenerating zones several weeks old during the later stages of myelination, nerve endings of terminal arborizations exhibit slow adjustments of retraction, extension, and branching. These are quite like similar adjustments that take place in normal zones of young growing tadpoles.

It is clear from these observations that nerve ending patterns are not necessarily fixed and stable. The changed conditions imposed by experimental injuries often cause marked adjustments of the endings which result in new patterns. Such adjustments probably also occur at some synapses between nerve cells within the central nervous system.

Illustrative ciné-photomicrographs have been obtained.

¹ Aided by a grant from the Penrose fund of the American Philosophical Society and a grant from the American Association for the Advancement of Science.

INTRODUCTION

DIRECT observations of nerve fibers in living frog tadpoles may be made. In favorable cases the delicate endings of cutaneous terminal arborizations of myelinated fibers may also be discerned. If the same nerve endings in a tadpole are watched from day to day a fairly complete record can be secured of any changes that may take place. Some records of this type have already been published. These reveal nerve ending adjustments in tadpoles during rapid growth in size (Speidel, '42) and also in tadpoles during and following irritative treatments with alcohol, metrazol, and other irritants (Speidel, '36, '40, and '41).

Additional case histories are presented in this account which show the nerve ending changes in tadpoles subjected to various experimental injuries. The acute type of injury and recovery is well illustrated by the electric shock experiments; the chronic type by the starvation experiments, and slow adjustments to a changing terrain by the regeneration experiments. Examples are also given of nerve ending behavior in tadpoles approaching metamorphosis and in tadpoles treated with insulin, chloretone, and heat.

Although a few observations on rapidly advancing nerve endings are described, this account deals chiefly with the mature resting endings of terminal arborizations of myelinated fibers. Endings of this type are concerned in the mediation of nervous activities of relatively refined nature. They are present not only at the skin but also at synapses between nerve cells within the central nervous system. Modifications of nerve endings, therefore, may cause profound functional effects on general nervous activities.

Tadpoles of *Pseudacris feriarum* and *Hyla crucifer* were used in these experiments. During microscopic examination an animal was placed in a special upright chamber and kept temporarily immobilized by weak chloretone solution. Ciné-photomicrographs were made from many of the experimental animals. Several of the illustrations are based upon motion picture records.

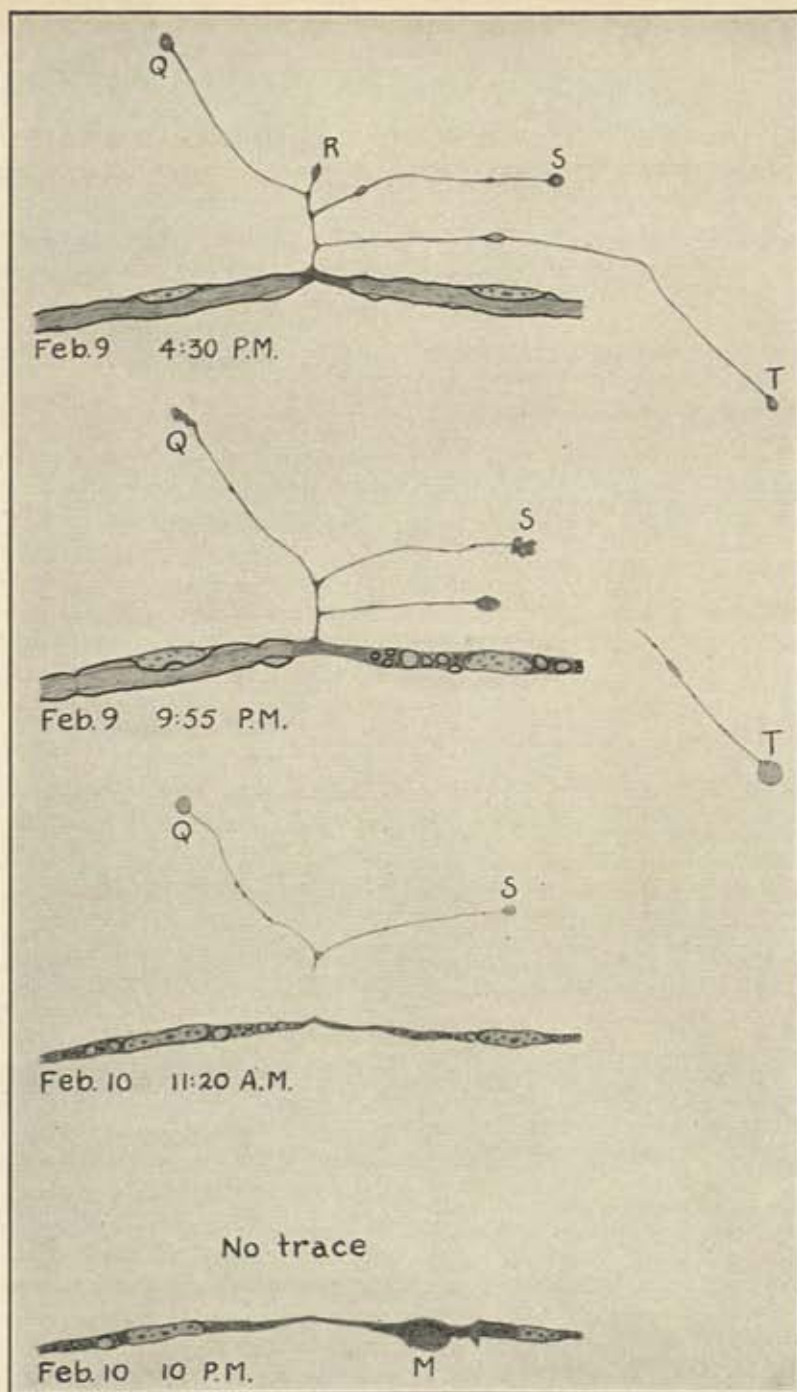


FIG. 1. Degenerative changes of the endings of a terminal arborization of the distal stump of a severed nerve fiber. Tadpole no. 1919, nerve fiber cut on February 9th at 4:18 P.M. The wound was some distance from the part of the fiber illustrated, a condition which ruled out the possibility of direct regional traumatic influences. Trophic changes quickly became visible within the first half hour. At 4:30 P.M. a vacuole was visible near the center of each of the four end bulbs. By 9:55 P.M. ending *R* had disappeared; the branch ending in *T* had suffered autotomy of its distal portion; and ending *S* was swollen and irregular in contour. One of the myelin segments had broken up into globules and the other was in process of fragmentation. On February 10th at 11:20 A.M. endings *Q* and *S* were still recognizable though they were disjoined from the remains of the main nerve fiber. The branches were very tenuous. They were characterized in some places by degenerative granules. By 10 P.M. there was no longer any trace of the terminal arborization. A macrophage (*M*) was active in ingesting myelin and axis cylinder remnants from within the neurilemma tube.

COMPLETE DEGENERATION OF NERVE ENDINGS OF TERMINAL ARBORIZATIONS

Either complete or incomplete degeneration may be exhibited by terminal arborizations of injured nerve fibers. Cases of complete degeneration sometimes occur spontaneously in the tadpole's tail, particularly as the time for metamorphosis approaches. Other cases have been noted in animals subjected to irritative treatments of appropriate severity, as after treatment with electricity, metrazol, alcohol, and insulin.

The principal steps in nerve ending degeneration are also readily seen in the distal stump portion of a sectioned myelinated fiber. In the example given (Fig. 1) a young terminal arborization arising at a node of Ranvier is shown as it undergoes complete trophic degeneration. The sketches show the condition of the nerve endings at the following intervals after the cut was made: 12 minutes, 5½ hours, 19 hours, and 30 hours. The regressive changes include early vacuolation of the end bulbs, swelling, development of irregular end bulb contours, granulation, and fragmentation of the branches.

Other records of terminal arborization degeneration have been obtained. Essentially the same sequence of changes is exhibited whether the degeneration is induced by nerve section or by other means.

HISTORIES OF NERVE ENDINGS IN TADPOLES SUBJECTED TO ELECTRIC SHOCKS

With the electric current practically any degree of irritation or injury to tadpole tissues may be induced. Very severe treatments cause death. Severe treatments which are not lethal may bring about the degeneration of variable amounts of nerve substance. Other tissues are also conspicuously damaged, particularly the muscle and epithelium. More moderate treatments may cause visible nerve irritation without being followed by any loss of nerve substance. Mild treatments may induce little or no nerve change.

A severely injured fiber may degenerate with destruction of both axis cylinder and myelin sheath. Its nerve endings are also lost. A less severely injured fiber may lose a number of its most distal myelin sheath segments even though the axis cylinder survives. The terminal arborization endings of such a fiber may, or may not, sur-

vive. Moderately injured fibers may exhibit swelling of the myelin sheath. This is occasionally accompanied by some loss of nerve ending substance. Mildly irritated fibers may develop temporary vacuoles between the myelin sheath and axis cylinder. Nerve endings of such fibers usually remain fairly constant, though some end bulbs may exhibit swelling.

A fine example of nerve fiber behavior after electric shock treatment is illustrated (Fig. 2). The injury in this case was moderately severe, enough to induce acute irritative effects in the nerve fiber figured. Swelling of the end bulbs and some loss of nerve ending substance ensued. The older more massive myelin sheath segments survived, although a young terminal one degenerated. Three days of recovery was sufficient to allow the development of a pattern of endings somewhat different from the original pattern at the time of the injury.

An even greater degree of injury may sometimes be induced in some of the nerve fibers of electrically shocked tadpoles. Particularly interesting fibers are those which lose some of their distal myelin sheath segments without, however, degeneration of the corresponding axis cylinder portion. Two regions of such a fiber are illustrated (Figs. 3 and 4). The first of these (Fig. 3) pictures three degenerating myelin segments together with the remains of two side branches at former nodes of Ranvier. Complete loss of the side branches followed. Myelin debris obscured somewhat the exact condition of the axis cylinder. Nevertheless, a sure indication that it survived was afforded by the survival of one of its terminal endings that emerged from the most distal myelin sheath segment. This feature is illustrated in Fig. 4, which also reveals the steps of recovery of the terminal branch during the eleven days following the injury.

Rapidly regenerating nerve tips are likewise readily affected by electric shock treatments. Several excellent cases have been watched in newly regenerated zones a few days after the tip of the tail has been cut off. One example is presented (Fig. 5) which clearly indicates that treatments of moderate severity are sufficient to stop an advancing growth cone temporarily. Furthermore, growth cones are affected by treatments mild enough to cause no visible change in the resting nerve endings in the normal unoperated tail zone of the same tadpole.

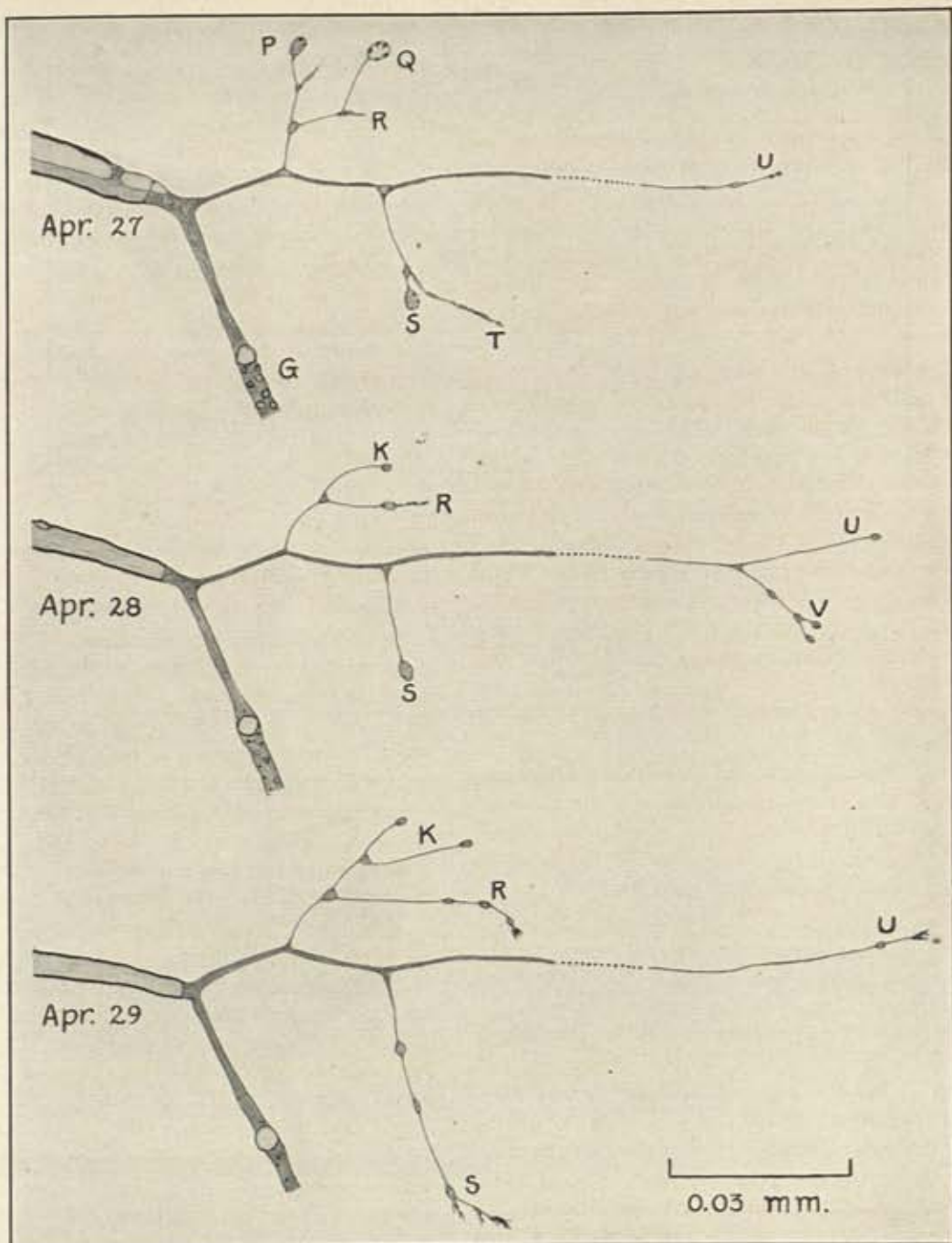


FIG. 2. Marked irritation of the endings of a terminal arborization following electric shock treatments and the subsequent steps of recovery. Tadpole no. 2432, subjected to a series of electric shocks on April 26th. The sketches are drawn exactly to scale from ciné-photomicrographic records. On April 27th the endings P, Q, and S were markedly swollen; T was degenerating and R was retracting. The myelin segment was greatly swollen, its diameter being more than twice that of the enclosed axis cylinder. The myelin globules at G represent the remains of a young delicate myelin segment which was just becoming differentiated on April 26th at the time of the injury. On April 28th endings P, Q, and T were no longer discernible, but new branches were present at K and V. Marked reduction of the myelin segment had taken place, so that it appeared essentially normal. By April 29th ending V had disappeared but ending K had branched and grown. Endings R, S, and U had all grown and at the time of observation each was provided with an active growth cone tip. (The dotted line indicates that a part of the length of the branch ending in U has been omitted from the drawing.) A distance of 0.03 mm (30 microns) is indicated below.

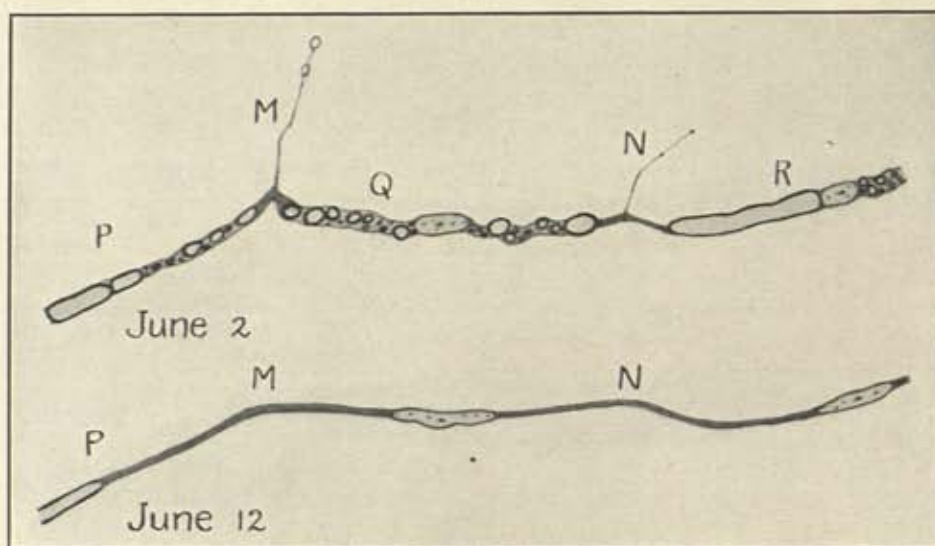


FIG. 3. Severe irritation of a myelinated fiber resulting from electric shock treatments with subsequent myelin segment degeneration and elimination of collateral branches. Tadpole no. 2452, subjected to a series of electric shocks on May 31st and June 1st. The injury was sufficient to induce breaking up of the myelin sheath of the 9 most distal segments of the fiber illustrated. *Q* represents the 4th myelin segment from the end, *P* the 5th, and *R* the 3rd. On June 2nd these segments exhibited fragmentation. At *M* and *N* are the greatly reduced remnants of what were terminal arborizations before the injury. By June 4th these had suffered complete elimination. The main axis cylinder portion of the fiber, however, survived. A much later condition of the fiber on June 12th is shown. New myelin segments were present on the proximal part of the fiber, just reaching the field illustrated at *P*. Collateral branches did not again develop at the former sites, *M* and *N*. (The history of the most distal part of this fiber is presented in Fig. 4.)

HISTORIES OF NERVE ENDINGS IN STARVED TADPOLES

General tissue injury progressively develops in tadpoles subjected to starvation. Typical irritative changes become discernible in nerve fibers and their endings. Marked irregularities may characterize the surface epithelium of the tail if the starvation period is prolonged. A chronic state of irritation is set up.

Nerve endings of irritated myelinated fibers may display swelling, retraction, and loss of nerve substance by degeneration. If the starvation period is not too long recovery readily takes place. The endings again become normal in appearance and some growth adjustments may occur.

The first case illustrated (Fig. 6) shows the changes in three endings of a young terminal arborization over a period of 12 days. During the first starvation period the endings retracted. This was followed by some growth and extension after food was made available. A second starvation period again initiated regressive changes in the endings.

The second case (Fig. 7) shows the changes in an ending belonging to a terminal arborization of the same myelinated fiber as that of the preceding figure (Fig. 6). The arborization in this case was located more distally along the fiber. As before regressive changes were exhibited by the ending during the periods of starvation. During the period of recovery after the ending had grown out some distance, however, retraction again occurred even though the food conditions at this time were suitable for further growth. This is merely an indication that an individual ending may undergo regressive change at the same time that other endings are either advancing or at least maintaining their positions. This point has been clearly brought out by some prolonged histories of growing terminal arborizations previously reported (Speidel, '42).

As a result of the chronic irritation of prolonged starvation, an end bulb may become greatly swollen. It may then suffer granular degeneration; or it may break away from the nerve ending and undergo autolysis; or it may suffer autotomy and be ingested by a macrophage. An interesting

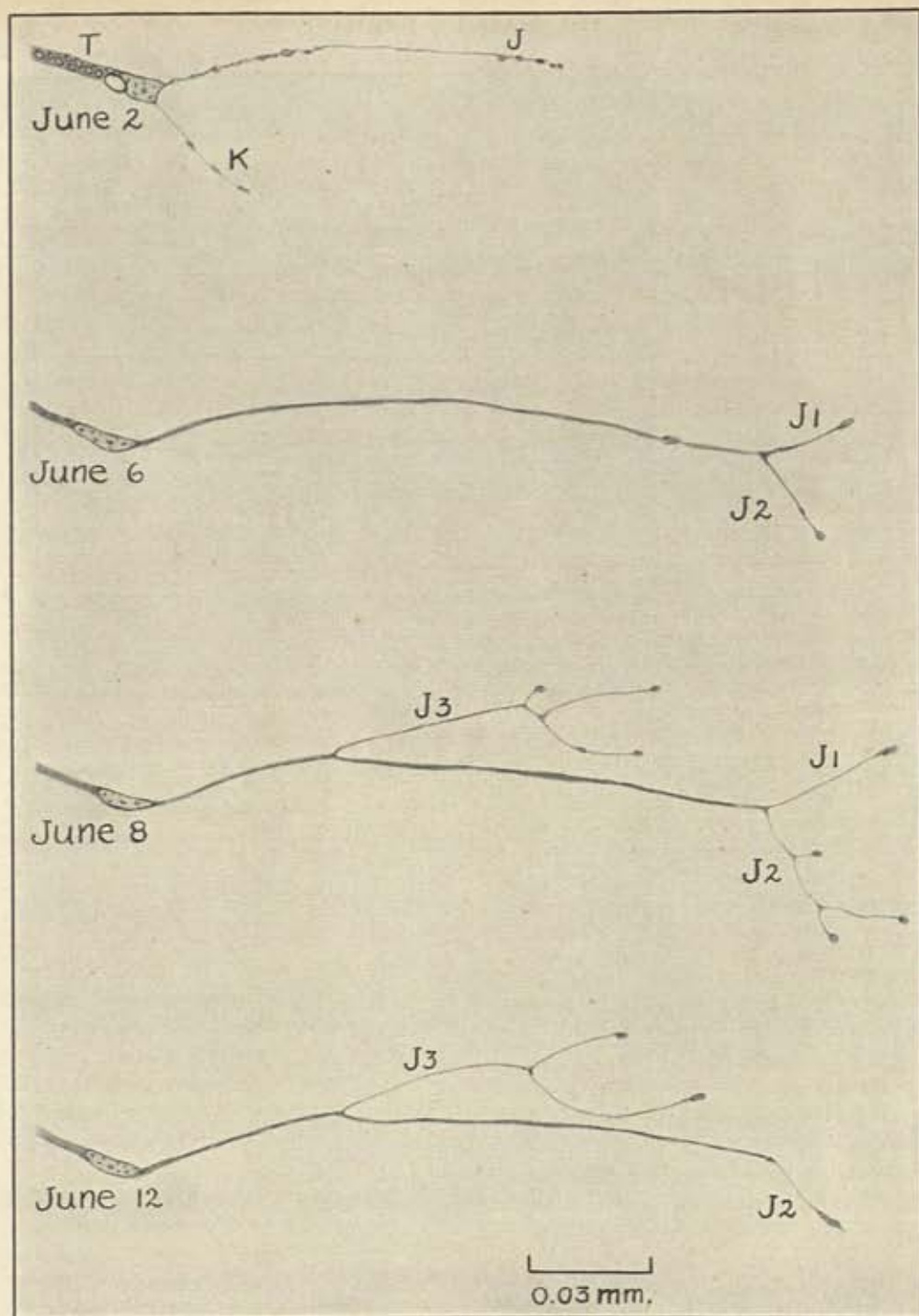


FIG. 4. Severe irritation of the terminal branches of a myelinated fiber resulting from electric shock treatments and the subsequent steps of recovery. Tadpole no. 2452, subjected to a series of electric shocks on May 31st and June 1st. The injury was sufficient to induce breaking up of the nine most distal myelin sheath segments. The sketches are drawn exactly to scale from ciné-photomicrographic records. On June 2nd two delicate irritated branches (*J* and *K*) were visible emerging from the degenerating terminal myelin segment (*T*). The sheath cell of this segment is located at the base of the two branches. During the next day ending *K* was lost completely; ending *J*, however, survived and grew. By June 6th it had extended and branched near its tip, forming *J1* and *J2*. On June 8th a third branch (*J3*) was present, and *J2* had given rise to two additional short endings. By June 12th, however, *J1* had been eliminated and a reduction in the number of endings of *J2* and *J3* had also taken place. A distance of 0.03 mm is indicated below. (The history of a more proximal portion of this same fiber is given in Fig. 3.)

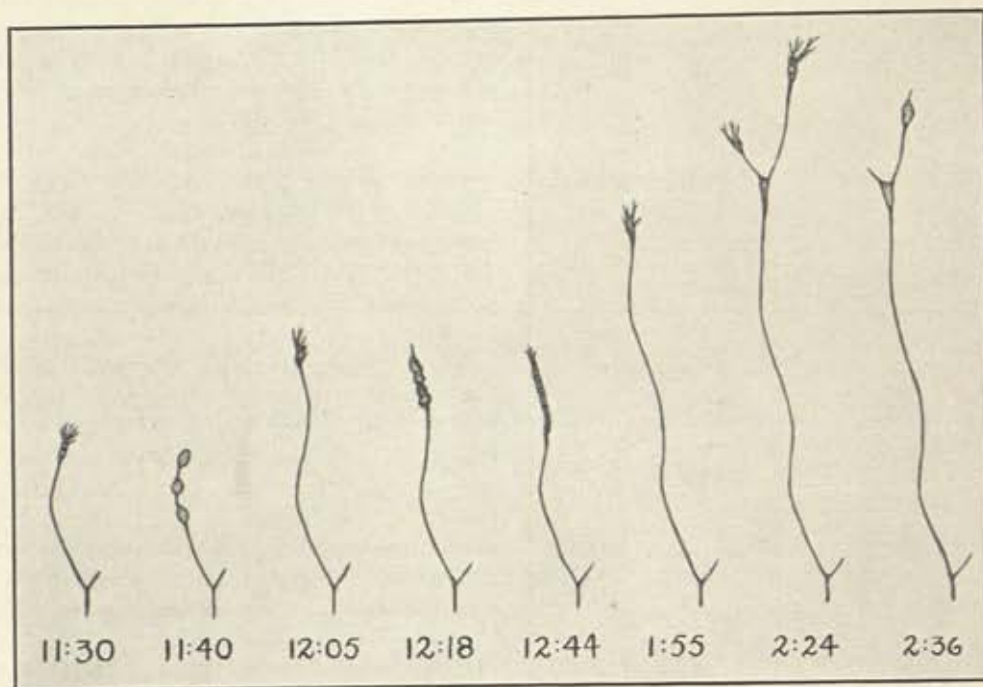


FIG. 5. Successive retraction and extension of a regenerating nerve ending, correlated with alternating periods of electric shock treatment and recovery. Tadpole no. 2422, subjected to electric shocks for a few seconds at 11:37 A.M., 12:08 P.M. (weak), 12:15 P.M., 2:04 P.M. (weak), and 2:33 P.M. The fiber illustrated was growing into the newly regenerating zone four days after removal of the tip of the tail. At 11:30 A.M. the nerve fiber tip was actively advancing. At 11:40 after the first electric treatment the tip became rounded and lost its delicate pseudopods. Two varicosities appeared proximally. Growth, however, was resumed within a few minutes and the tip advanced to the position shown at 12:05. A weak treatment followed by a stronger one caused the formation of a typical retraction club at 12:18. Growth was inhibited for nearly a half hour. At 12:44 the tip is just beginning its transformation back into a growth cone. Further growth took place as illustrated at 1:55 P.M. and 2:24 P.M. A weak electric treatment at 2:04 P.M. failed to stop the advancing growth cone. Extension and branching took place as indicated at 2:24 P.M. A final electric treatment caused retraction of both tips within a few minutes at 2:36 P.M. Recovery and further growth then followed along both branches and by the following day both tips had extended long distances.

example is given (Fig. 8) in which a swollen end bulb underwent autotomy and was taken up at once by a macrophage. At the new nerve tip an abortive growth cone developed, but it soon became transformed into an irritated resting end bulb.

HISTORIES OF NERVE ENDINGS IN OR NEAR REGENERATING ZONES

In previous papers (Speidel, '33 and '35) an account has been given of the behavior of the rapidly advancing nerve tips in newly regenerating zones. Therefore, these need not be considered here. In older zones of regeneration some fibers become provided with myelin sheath segments. Terminal arborizations of nerve endings arise at some of

the nodes of Ranvier. Such arborizations of endings exhibit growth adjustments as the regenerating zone becomes more mature.

There is no essential difference between the growth adjustments of arborizations of regenerating zones and those of normal zones. In another paper (Speidel, '42) the adjustments of terminal arborizations during normal tadpole growth have been described. The endings in regenerating zones seem somewhat less stable and the arborizations are less complex, *i.e.*, they comprise fewer branches and endings.

One case is presented here (Fig. 9) which shows the main changes over a period of 21 days. Retraction and loss of one ending and the genesis and growth of another take place. At the same time various adjustments of the myelin sheath

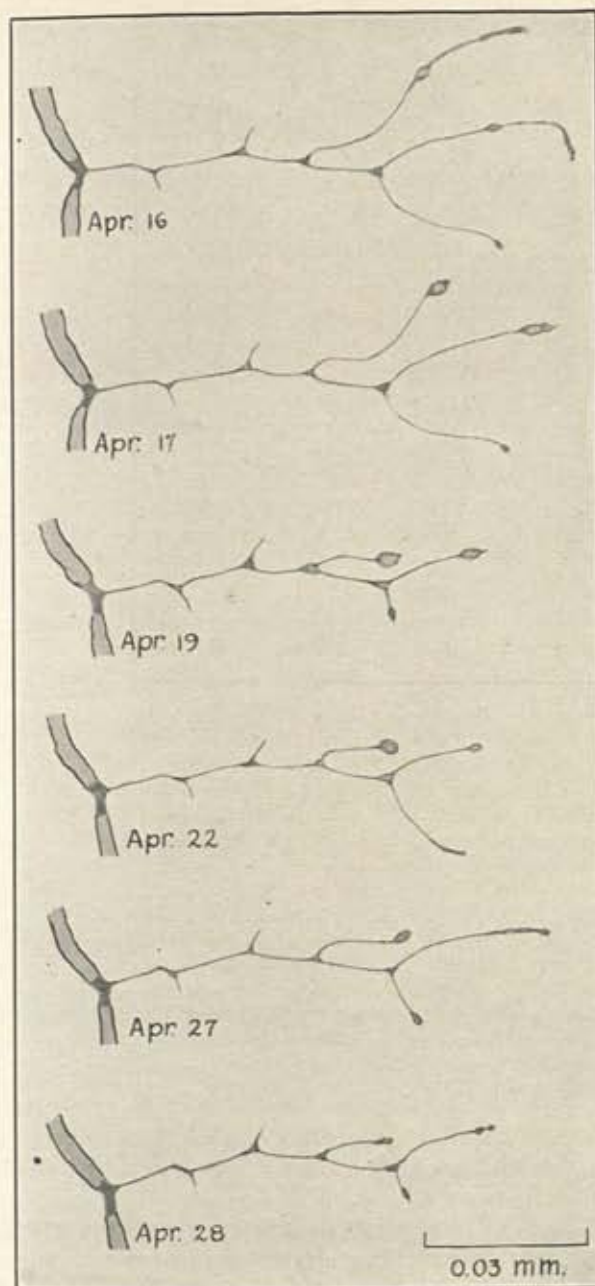


FIG. 6. Retraction and extension of nerve endings correlated with periods of starvation and good nutrition. Tadpole no. 2419, starved from April 16th to 20th and from April 27th to 29th; food available at other times. The sketches are drawn exactly to scale from motion picture records. On April 16th in a young tadpole three endings of a terminal arborization were observed, two of which were advancing. On the following day these two were retracting, their tips being in typical swollen retraction club state. By April 19th marked retraction by all three endings was apparent. By April 22nd after food was available the lower ending had recovered and grown out, and by April 27th the middle ending also had grown.

segments at the base of the terminal arborization occur. Possibly the myelin sheath adjustments are responsible for the elimination of one of the side branches (branch J).

Two other endings of the same arborization were also watched, although these have not been included in the sketches. Each of these exhibited limited changes from day to day of both extension and retraction at the tips. The net result, however, was relatively little change in position of the end bulbs.

Nerve endings close to a wound suffer irritation. They may swell and retract slightly. As wound repair proceeds and as the tissues undergo regulation and regeneration, the irritated nerve endings also recover. At times growth and branching take place. The presence of the adjacent regenerating tissues seems to stimulate progressive changes in the nerve endings. This is well illustrated by the example given (Fig. 10).

HISTORIES OF NERVE ENDINGS UNDER VARIOUS OTHER CONDITIONS

A few other observations and experiments on nerve endings deserve brief mention. These include nerve ending behavior in tadpoles approaching metamorphosis, and in tadpoles subjected to treatments with chloretone, alcohol, hot water, hypertonic salt solution, and insulin.

As a tadpole approaches the time for metamorphosis, regressive changes take place in the tail. Reduction in size of the tail proceeds and the circulation is markedly affected. Conspicuous structural changes are noticeable in the epithelium, muscle, and nerve. Many endings of terminal arborizations exhibit swelling and slight retraction. These are typical irritative changes that parallel the early degenerative changes in the tail, an appendage that is soon to be resorbed. Occasionally, however, a nerve ending grows while the tail as a whole is being reduced in size. The case illustrated (Fig. 11) shows an advancing ending over a 4-day period just before the tail was lost and metamorphosis completed. In another tadpole a large growth cone was noted in the degenerating tail only 2 days before the animal left the water (Fig. 14). Growth was very slight in this case.

On April 28th after a second starvation period all three endings exhibited some retraction. A distance of 0.03 mm is indicated below. (The history of an ending belonging to the same myelinated fiber located nearer the tip of the tail is given in Fig. 7.)

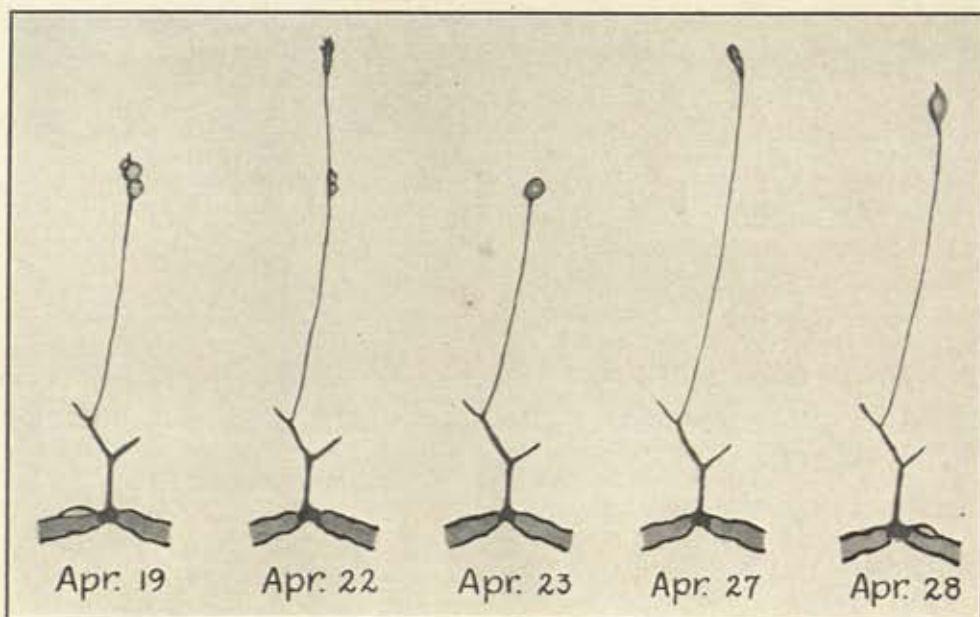


FIG. 7. Retraction and extension of a nerve ending correlated with periods of starvation and good nutrition. Tadpole no. 2419, starved from April 16th to 20th and from April 27th to 29th; food available at other times. The sketches are drawn exactly to scale from motion picture records. On April 19th after three days of starvation a swollen irritated ending was visible, as indicated. After food became available this ending grew out and on April 22nd it was slowly advancing. On April 23rd, though food was still available, it retracted to its former location. By April 27th growth again had taken place. On April 28th after another period of starvation it again exhibited swelling and some retraction. (The history of endings belonging to the same myelinated fiber located farther proximally is given in Fig. 6.)

In a previous paper (Speidel, '36) I have pointed out that the resting endings of terminal arborizations exhibit less conspicuous changes during alcoholic intoxication than do the growing endings of regenerating fibers. Chloretone anesthesia experiments bring out the same difference. One example is cited (Fig. 12) which clearly demonstrates the stability of resting endings throughout alternating periods of deep and light chloretone anesthesia during which a growing ending exhibited alternating extension and retraction.

If a tadpole is immersed in water heated to a temperature of more than 37°C nerve fibers become irritated. An actively advancing growth cone of a regenerating fiber may become transformed into a retraction club. Swollen varicosities may also appear along the irritated fiber. One example is illustrated (Fig. 13). In this case a growing tip retracted slightly after the first heat treatment. It then grew and gave rise to two branches as recovery took place. A second brief heat treatment temporarily stopped the advance of each of the growing tips and caused some swelling. With the restoration of normal conditions reduc-

tion of swelling and further growth of the endings occurred within a short time.

I have watched the same kind of changes in growing nerve fibers in tadpoles subjected to suitable irritative treatments with hypertonic sodium chloride solution. Similar changes have also been described with electric shock treatments (*cf.* Fig. 5), with alcohol (Speidel, '36), with metrazol (Speidel, '40), with chloretone (*cf.* Fig. 12), and with insulin (*cf.* Fig. 16).

Nerve fibers usually cease growing in moribund tadpoles. As the blood circulation slows or stops entirely, growth cones round up or become transformed into retraction clubs. Retraction often takes place. Nevertheless, occasionally an actively growing nerve tip is present in a regenerating zone of an animal approaching death even though all other nerve tips exhibit regressive change. The case illustrated (Fig. 15) was observed in a tadpole subjected to severe alcoholic intoxication. Another case practically similar in nature was observed in a tadpole subjected to severe chloretone anesthesia.

Many tadpoles have been subjected to insulin

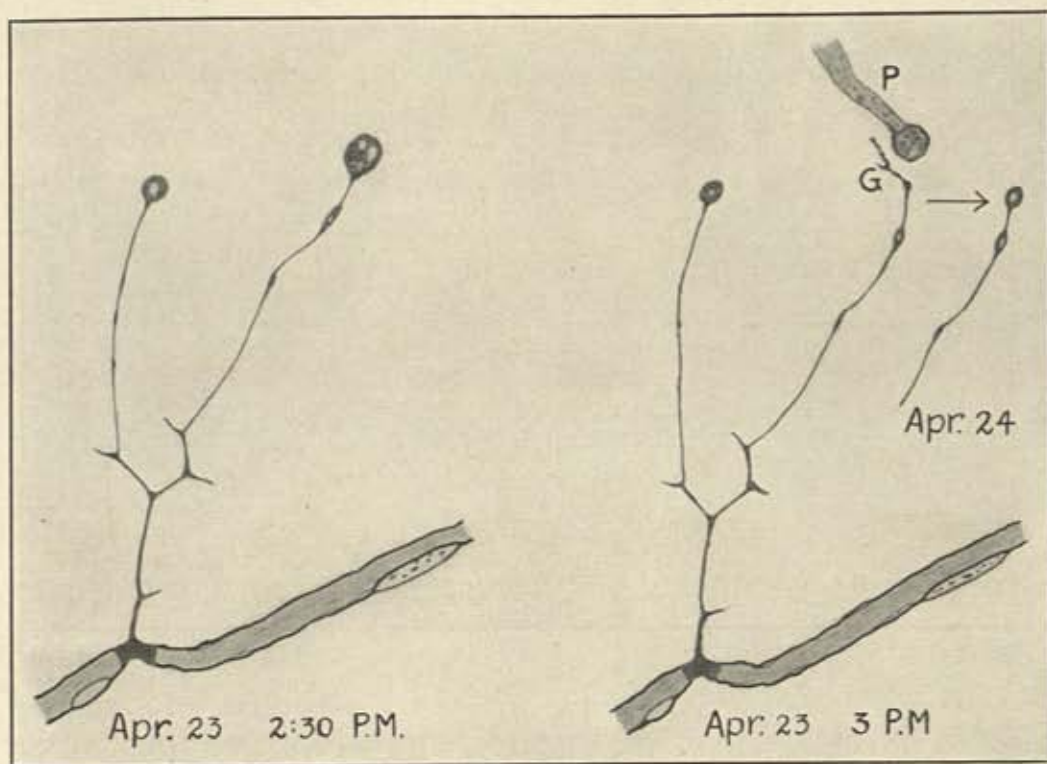


FIG. 8. Autotomy and phagocytosis of the swollen tip of a nerve ending after prolonged starvation. Tadpole no. 1541, regenerating zone following partial tail amputation on March 24th, starved from April 12th on. A motion picture record of this case was obtained. On April 23rd at 2:30 P.M. after eleven days of starvation two swollen tips of nerve endings were observed, branches from an irritated myelinated fiber. One of these during the next half hour suffered autotomy and was ingested by a macrophage, the long process (*P*) of which is figured. A new growth cone (*G*) developed at the tip of the ending and grew slightly at first, but later retracted. On April 24th the tip again was rounded and swollen, as indicated by the arrow.

treatments of various degrees of severity. The insulin extract was not injected; the animals were merely immersed in solutions of suitable strengths. The treatments caused injury to the epithelium and to other tissues. Practically any degree of neuritis could be induced.

Two cases are selected for illustration. The first of these (Fig. 16) shows the advancing growth cone of a regenerating fiber which, with insulin treatment, becomes transformed into a retracting nerve tip. The retraction is temporary. Growth is again resumed soon after normal conditions are restored. The second case (Fig. 17) shows a few highly irritated endings of a myelinated fiber. Each of the three end bulbs pictured is swollen and vacuolated. The parent fiber also displays vacuoles between the myelin sheath and axis cylinder. Nerve fibers in such a condition may recover readily provided the insulin treatment is not continued too long.

CINÉ-PHOTOGRAPHIC RECORDS OF NERVE ENDING HISTORIES

Besides those already referred to in previous papers, many ciné-photomicrographic records have been obtained of nerve ending adjustments in tadpoles subjected to various injurious treatments. These motion pictures portray cases from tadpoles subjected to electric shocks, insulin, chloretone, starvation, hypertonic salt solution, and wound inflection caused by cutting. Several of the figures of this paper (*e.g.*, Figs. 2, 3, 4, 6, 7, 8, 9, 11, 14, and 17) have been sketched from records of this sort. The subjects of some of the pictures follow:

1. Response of several branches of a terminal arborization to electrical injury. Irritative changes in the endings are shown on the days following a series of electric shocks. Recovery changes during the next two days are also portrayed. Changes in myelin segments during irritation and recovery are also pictured in this case.

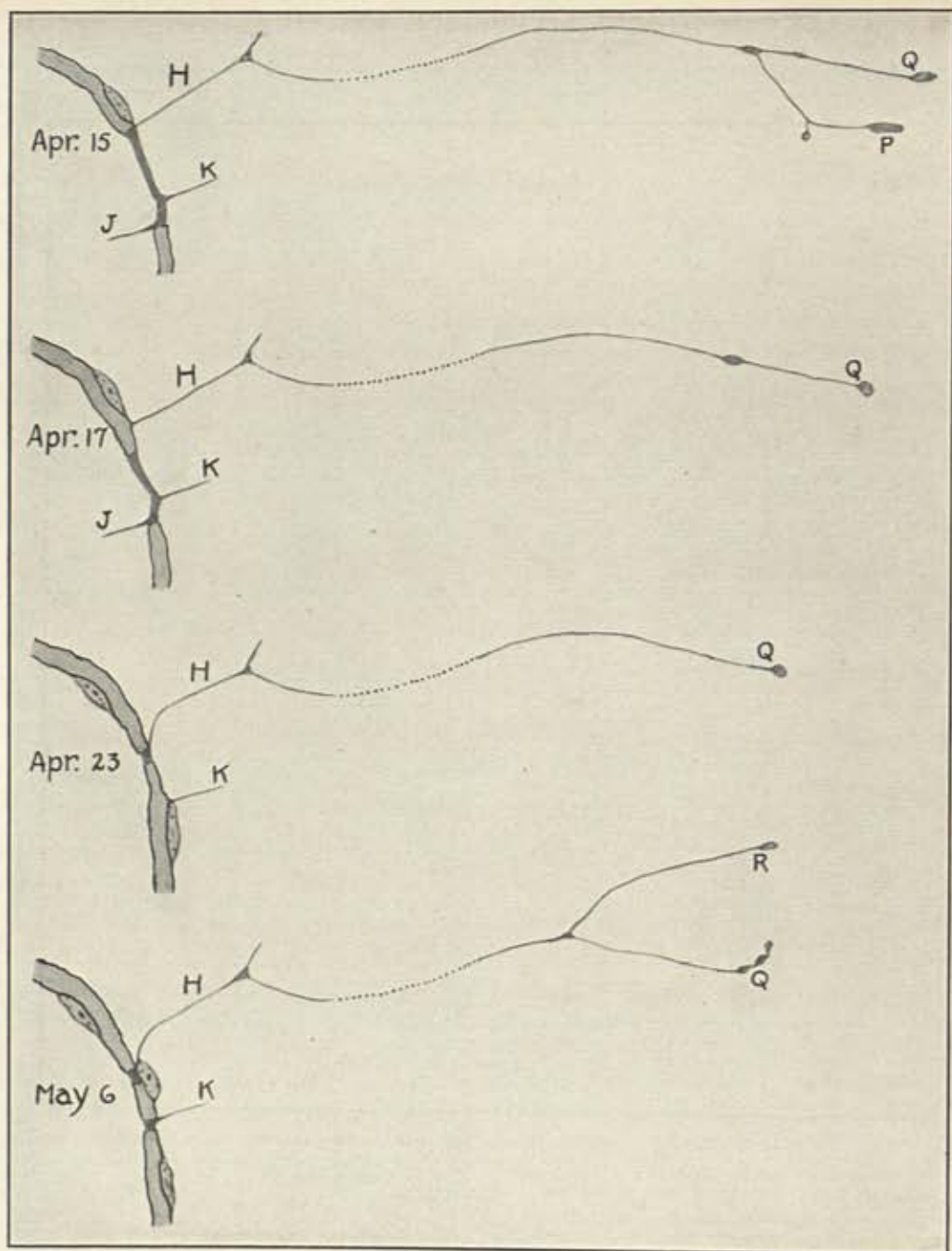


FIG. 9. Nerve ending adjustments during myelination in a regenerating zone. Tadpole no. 2417, regenerating zone following partial tail amputation on March 31st. On April 15th after fifteen days of regeneration two endings (P and Q) were observed which belonged to a collateral (H) of a newly myelinated fiber. J and K represent the bases of two other collateral branches. The myelin segment below J was the terminal segment of the fiber. During the next two days ending P underwent retraction and on April 17th was completely gone. New myelin was formed extending beyond the base of H. During the next six days myelin sheath adjustments occurred. New myelin was formed in such a manner that the base of branch H was pushed distally a short distance; branch J was eliminated; and the fiber between H and K became ensheathed with myelin belonging to the lower segment. Ending Q retracted a short distance. By May 6th a new branch R had made its appearance and grown to the position shown; ending Q shifted slightly. The myelin between H and K together with a new sheath cell formed a new short segment. During the period of observation from April 15th to May 6th four new myelin segments also were formed at the peripheral end of the fiber illustrated. (The dotted line indicates that a part of the length of the fiber has been omitted from the drawing.)

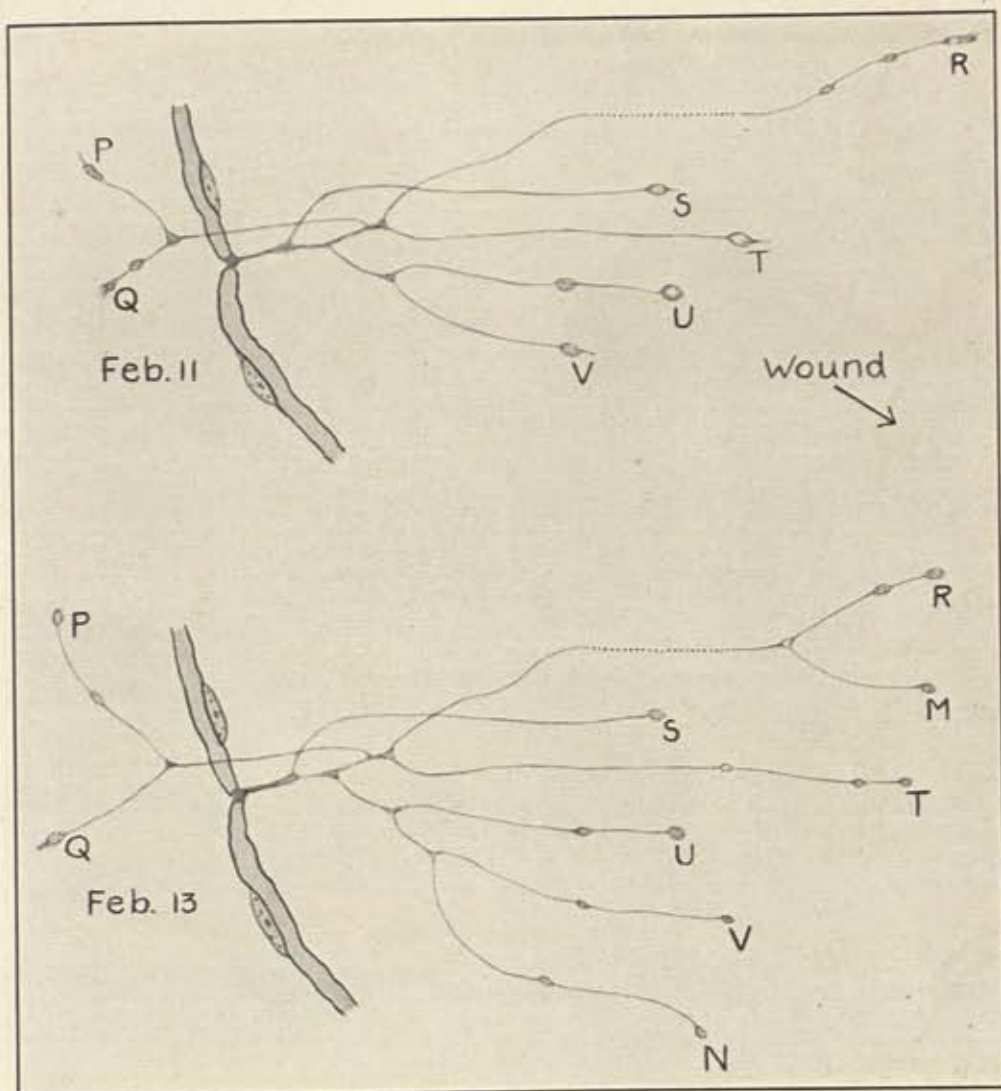


FIG. 10. Recovery of the endings of a terminal arborization located at the proximal edge of a wound. Tadpole no. 1918, ventral fin in the direction of the arrow wounded by cutting on February 9th. The myelinated fiber illustrated was severed by the cut, but the portion figured was on the proximal side of the wound and did not degenerate. During the next two days irritative changes of swelling and retraction were visible in the endings of the terminal arborization, as general tissue regulation took place. On February 11th retraction clubs were present on endings *P*, *S*, *T*, and *V*. A swollen tip characterized ending *U*. Ending *Q*, however, was provided with a growth cone that displayed typical ameboid motion. Correlated with wound healing of the next two days, recovery changes were exhibited by the branches of the terminal arborization. On February 13th all endings except *Q* and *S* were of the usual spherical resting type. Endings *P*, *Q*, *T*, and *V* had grown some. Two entirely new branches, endings *M* and *N*, had developed in the positions shown. (The dotted line indicates that a part of the length of the branch ending in *R* has been omitted from the drawing.)

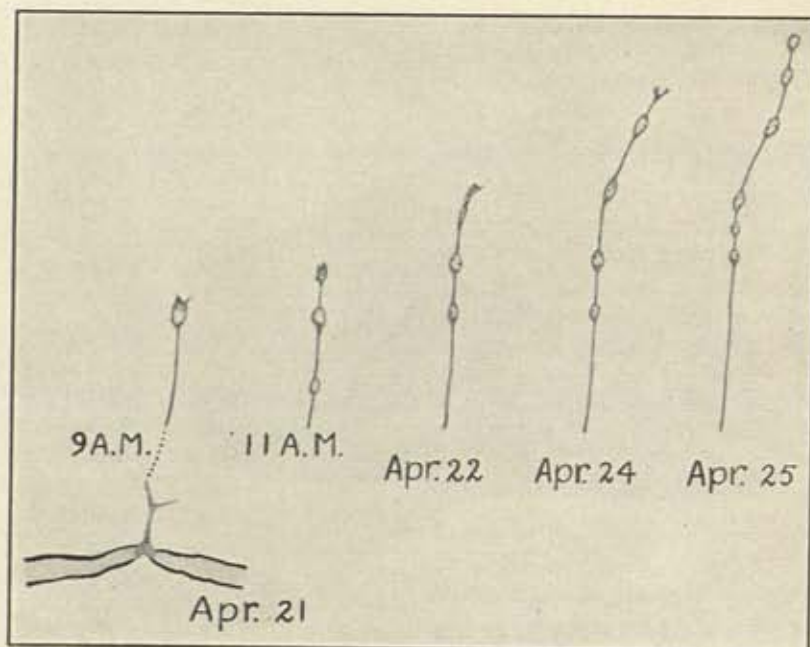


FIG. 11. Growth of a nerve ending in a tadpole nearing the time for metamorphosis. Tadpole no. 2247, with large hind limbs and with its tail beginning to show degenerative changes. The sketches are made exactly to scale from motion picture records. On April 21st at 9 A.M. a swollen nerve ending was observed. (The dotted line indicates that a part of its length has been omitted from the drawing.) The ending slowly advanced and reached the position shown at 11 A.M. Further advance took place during the next few days, its position being shown on April 22nd, 24th, and 25th. The total advance measured 40 microns. At the same time some reduction in the size of the tail occurred. On April 26th both fore limbs had appeared and the tail was greatly reduced in size. On April 27th the tadpole left the water and metamorphosis was nearly complete.

2. Effects of severe electrical injury on some of the endings and myelin segments of a nerve fiber. Irritative and degenerative changes are recorded for some endings and myelin segments. Growth and branching of a surviving ending are pictured on the 1st, 5th, 7th, 11th, and 13th days after the injury. Complete loss of several myelin segments is shown.

3. Examples of swollen and retracting end bulbs at the tips of arborization branches in a badly injured tadpole on the day following electrical treatment. Death of the animal in this case ensued two days after the injury.

4. Acutely irritated myelin segments during the first few hours after electrical injury. Vacuolation and myelin ovoid formation are illustrated both in tadpoles that recover from the treatment and in those that later succumb.

5. Effects of electric shocks on actively advancing growth cones of regenerating nerve fibers four days after tail section.

6. Effects of electric shocks on epithelium, muscle, blood vessels, blood cells, and pigment.

7. Several examples showing the characteristic

irritative effects of starvation on nerve endings and on myelin segments.

8. Several cases illustrating the recovery of irritated nerve endings in tadpoles after periods of starvation from three days to three weeks.

9. Swelling, autotomy, and phagocytosis of an end bulb in a tadpole starved for eleven days. Removal of the end bulb was followed by development at the tip of an abortive growth cone.

10. History of several terminal arborization endings in a regenerating zone 15 to 40 days after tail section. Swelling, retraction, and complete elimination of some endings are illustrated, as well as extension and branching of others.

11. Examples of swelling and retraction of endings of myelinated fibers in tadpoles approaching metamorphosis.

12. Examples of advance of endings in tadpoles approaching metamorphosis which already display noticeable tail reduction.

13. Examples illustrating characteristic regressive changes in nerve fiber endings and myelin segments in tadpoles subjected to suitable treatments with the

following: insulin, methyl alcohol, chloretone, lead acetate, hypertonic sodium chloride solution, and heat.

14. Macrophage taking up a myelin globule from an injured nerve fiber, eight hours after the tadpole was subjected to an insulin treatment.

COMMENTS

It is clear from the preceding case histories that a great deal of adjustment is possible in the peripheral distribution of cutaneous nerve endings in injured tadpoles. The general mechanism of change underlying such adjustments is the same regardless of the type of injury. Regressive change is characterized by swelling of end bulbs, retraction, and degeneration. Degeneration may involve only the most distal portion. Recovery change is characterized by reduction of swelling, extension, and the genesis of new branches. Since the endings are unsheathed, the pattern of an arborization after injury and regeneration is usually not exactly the same as the original pattern.

Furthermore, if free nerve endings at the skin are subject to adjustments of this sort, it follows that free nerve endings located elsewhere in the body may behave in like manner. Within the central nervous system free nerve endings are present in large numbers. They link nerve cells at synapses. Strong irritations might break some synapses by causing retraction or degeneration of some of these endings. With recovery new synaptic connections might be established.

Electric shock and insulin treatments markedly affect cutaneous endings in tadpoles. It seems probable that they profoundly affect synaptic endings in the brain. Such changes in human mental patients under treatment for mental disorders would afford an adequate anatomical basis for the observed changes in mental outlook that sometimes result. This interpretation is like that already advanced after an experimental study of the effects of metrazol on nerve fibers (Speidel, '40).

SUMMARY

1. Case histories are presented of individual nerve endings of terminal arborizations of myelinated fibers in frog tadpoles subjected to various kinds of injurious treatments. Electric shocks, starvation, chloretone anesthesia, wound inflac-

tion, insulin, and heat have each been used to induce nerve ending irritation.

2. Swelling, retraction, and variable amounts of degeneration characterize markedly irritated endings. Reduction of swelling, extension, and branching characterize endings in process of recovery.

3. Changes associated with chronic neuritis, such as are induced by starvation, are essentially similar to those associated with acute neuritis, such as are induced by electrical injury.

4. Examples are also presented of the behavior of rapidly growing nerve tips in young regenerating zones, as these are subjected to acute irritative treatments of several kinds.

5. In regenerating zones several weeks old during the later stages of myelination, nerve endings of terminal arborizations exhibit slow adjustments of retraction, extension, and branching. These are quite like similar adjustments that take place in normal zones of young growing tadpoles.

6. It is clear from these observations that nerve ending patterns are not necessarily fixed and stable. The changed conditions imposed by experimental injuries often cause marked adjustments of the endings which result in new patterns. Such adjustments probably also occur at some synapses between nerve cells within the central nervous system.

7. Illustrative ciné-photomicrographs have been obtained.

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EXPLANATION OF PLATE I

FIG. 12. Absence of visible change in the endings of a terminal arborization during chloretone treatment severe enough to induce retraction of the growth cones of regenerating fibers. Tadpole no. 1706, subjected to strong chloretone treatment from 9:37 A.M. to 9:52 A.M. and from 10:33 A.M. to 10:53 A.M. At other times the tadpole was immersed in either pond water or very weak chloretone solution. At the right of the figure is illustrated the growing ending of a nerve fiber in the rapidly regenerating tail tip zone, four days after tail section. At the left of the figure is illustrated the resting endings of a terminal arborization in the normal unoperated tail zone. The regenerating ending exhibited typical retraction during the strong chloretone treatments, as shown at 9:49 A.M. and 10:45 A.M. At other times this ending was provided with a growth cone which slowly advanced. The terminal arborization endings, on the other hand, exhibited practically no change throughout the treatments (except perhaps very slight vacuolation).

FIG. 13. Retraction and recovery of a regenerating ending correlated with heat treatments. Tadpole no. 1551, regenerating zone four days after tail section, immersed in hot water (40°–41° C) for brief periods of less than one minute at 10:15 A.M. and at 11:51 A.M. The advancing tip of a regenerating nerve fiber was observed at 10:05. Swelling and some retraction took place after hot water treatment, as shown at 10:20. During the next ninety minutes growth was resumed and the ending branched into two, as shown at 11:50. A second treatment with hot water again caused some retraction and the formation of swollen varicosities, as shown at 11:55. Ten minutes later at 12:05 both endings exhibited recovery and were again advancing.

FIG. 14. Advance of a nerve ending in a metamorphosing tadpole. Tadpole no. 2409, tail markedly reduced in size, all four limbs visible. On May 5th in a tadpole which exhibited pronounced degenerative changes in the tail a nerve ending provided with a blunt growth cone

was observed. On May 6th this had advanced a short distance in spite of the fact that the tail was undergoing rapid involution. On May 7th the animal left the water, tail resorption being far advanced.

FIG. 15. Advance of a regenerating nerve ending in a moribund alcohol-treated tadpole after cessation of the blood circulation. Tadpole no. 1514, regenerating zone four days old, immersed in 2 per cent alcohol from 11:23 A.M. to 1:15 P.M. At 12:43 an active growth cone was noticed at the tip of a fiber. All other regenerating tips of nerve fibers in the vicinity were in various stages of retraction. (One that was kept under observation retracted 25 micra between 11:44 and 12:42.) The growth cone illustrated, however, rapidly advanced during the next half hour reaching the position shown at 1:13, an advance of about 30 micra. Blood circulation in the tail ceased at 12:25 and was not resumed thereafter.

FIG. 16. Retraction of the tip of a regenerating nerve fiber in an insulin-treated tadpole, followed by growth of the nerve tip during recovery. Tadpole no. 2429, regenerating zone four days old, immersed in insulin solution from 9:26 A.M. to 10:10 A.M. An advancing growth cone at the tip of a regenerating fiber at 9:15 was transformed during insulin treatment into a retracting tip, as shown at 9:55. After replacement of the tadpole in pond water for about twenty minutes the nerve fiber tip resumed its advance, reaching the position shown at 11:15. Although the treatment injured the epithelium somewhat the tadpole survived without difficulty.

FIG. 17. Irritative changes in the endings of a myelinated fiber in an insulin-treated tadpole. Tadpole no. 2412, immersed in strong insulin solution for twelve minutes. A motion picture record of this case was obtained. One hour after the treatment, each of the three end bulbs shown in the illustration exhibited swelling with a centrally located vacuole. Two of the endings terminated in a short pointed filament. Vacuoles were also conspicuous in several places along the myelin segment where separation of the axis cylinder and myelin sheath had taken place.

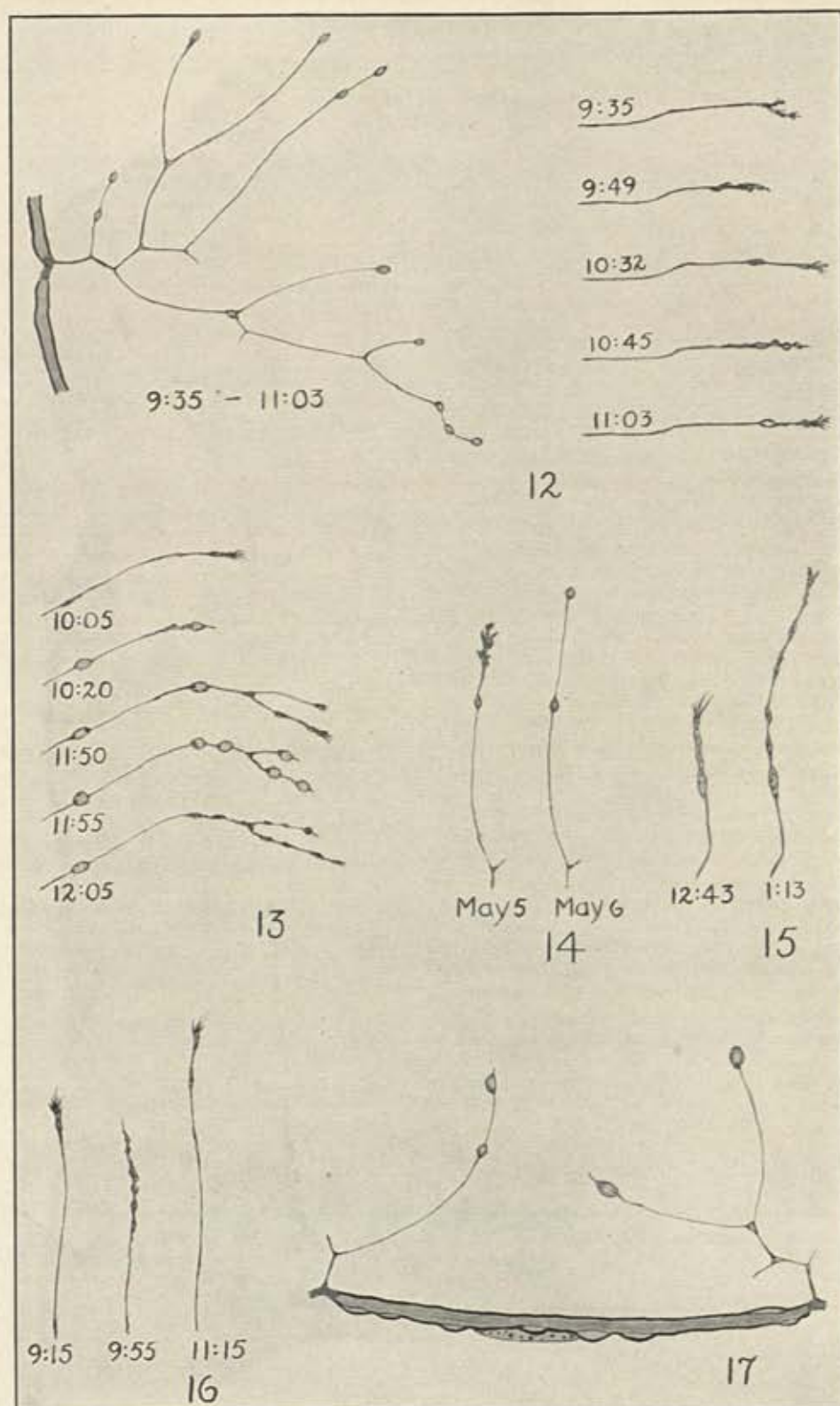


PLATE I

NEW MUTATIONAL SEGREGATIONS FROM *OENOTHERA* MUT. *ERYTHRINA* DE VRIES¹

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CONTENTS

Introduction	183
Historical	184
The normal progeny of <i>Oe. mut. erythrina</i>	185
<i>Oenothera</i> mut. <i>pollicata</i> as a recurrent segregate from <i>Oe. mut. erythrina</i>	187
<i>Oenothera</i> seg. <i>petiolaris</i> , seg. nov.	187
<i>Oenothera</i> seg. <i>contracta</i> , seg. nov.	195
<i>Oenothera</i> seg. <i>cyanea</i> , seg. nov.	201
<i>Oenothera</i> seg. <i>diminua</i> , seg. nov.	203
<i>Oenothera</i> seg. <i>elongata</i> , seg. nov.	206
<i>Oenothera</i> seg. <i>retracta</i> , seg. nov.	207
<i>Oenothera</i> seg. <i>sublethalis</i> , seg. nov.	209
Discussion and conclusions	209
Summary	212
Literature cited	214

ABSTRACT²

New mutational segregations from *Oenothera* mut. *Erythrina* de Vries: GEORGE H. SHULL. *Oe. mut. erythrina* de Vries, when selfed, is known to produce in every progeny two types, one repeating the parent, the other a new type, seg. *decipiens*, which breeds true when selfed because it lacks both of the balanced lethals which characterize *Oe. Lamarckiana*. *Erythrina* splits in this way because it has only one of the *Lamarckiana* lethals. Some years ago I reported the occurrence of a new mutational segregation in which mut. *pollicata* was found to characterize the *decipiens* component of such a splitting progeny, while normal hypanthium, styles and stigmas characterized the *erythrina* component. A continuation of studies with *erythrina* have brought to light a number of new segregations, sometimes replacing *decipiens*, in other cases being additional to *decipiens*. The first of these new mutational segregates was discovered on March 8, 1935, when family 3485, produced from a self-fertilized *erythrina* mother, was observed to split out 45 plants of a peculiar new type afterwards called seg. *petiolaris*, in a total progeny of 164. A complete analysis of this family showed it to consist of 70 *erythrina*, like the parent, 50 seg. *decipiens*, 43 seg. *petiolaris*, and 1 unidentified mutant. Over half of the *erythrina* plants in such a family repeat the three-way split when selfed, while the rest split only to *erythrina* and *decipiens*. On March 20, 1938, another remarkable new segregation, seg. *contracta*, was discovered in family 37428, derived from an *erythrina* mother in this same strain. The unique feature this time was not alone

the remarkable modification represented by the new type itself, but seg. *contracta* replaces seg. *decipiens*. Family 37428 consisted of 61 *erythrina* and 40 *contracta*, no *decipiens* being present. Every *erythrina* plant in such a family produced the same kind of a family, consisting of *erythrina* and *contracta*. In 1939 another new segregate, seg. *diminua*, was found, and in 1940, still another, seg. *cyanea*, was added to a *contracta*-segregating family (39533) which split to 61 *erythrina*, 25 *contracta*, 16 *cyanea*. In 1941 one family (40110) from selfed *erythrina* has had the *decipiens* segregate replaced by seg. *elongata* and in another progeny (40130) seg. *retracta* has replaced seg. *contracta*. An essentially true-breeding *erythrina* has resulted when seg. *decipiens* is replaced by seg. *sublethalis*, the latter being rarely seen because it has so little chlorophyll that usually it does not live beyond the germination stage. This "non-splitting" *erythrina* was discovered in 1938 in family 37411, but seg. *sublethalis* was not observed until the current year (1941).

INTRODUCTION

It is now well known that the mutations discovered in the *Oenotheras* by Hugo de Vries and subsequent workers are of several different kinds, including gene mutations as well as several different sorts of chromosomal aberrations. Several of these chromosomal irregularities result in characteristic changes in chromosome numbers, such as trisomics with 15 chromosomes, triploids with 21, tetraploids with 28, instead of the 14 which are normally present in *Oe. Lamarckiana* and in all of the known wild species of *Oenothera*.

The present paper deals with the genetical behavior of a mutant which is produced by a chromosomal aberration of a different kind, which affects the arrangement of the chromosomes without changing their number. There are four well-known mutants of this character, beginning with *Oe. mut. rubrinervis*, followed by *Oe. mut. erythrina*, *Oe. mut. rubricalyx* and *Oe. mut. rubricalyx* "Afterglow." These differ from *Oe. Lamarckiana*, from which they have been derived, in two very fundamental particulars, namely, (1) a reduction of the circle of 12 chromosomes of *Lamarckiana* to a circle of 6 or a circle of 8, the remaining chromosomes required to make up the typical 14 occurring in separate pairs, 3 pairs if the circle includes 8 chromosomes, or 4 pairs if

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the circle consists of 6 chromosomes; and (2) a loss of one of the balanced zygote lethals which give *Lamarckiana* the remarkable ability to breed true, notwithstanding the fact that every plant of *Lamarckiana* is a heterozygote.

This loss of one lethal factor makes possible the appearance of a homozygous segregate as a feature of the progenies of every self-fertilized plant of one of these mutants. The remaining lethal keeps *rubrinervis*, *erythrina*, *rubricalyx* and *rubricalyx* "Afterglow" just as permanently heterozygous as *Lamarckiana* itself, but instead of breeding true, *Oe. mut. rubrinervis* produces a progeny consisting of *rubrinervis* and *deserens*; *erythrina*, a progeny containing *erythrina* and *decipiens*; and *rubricalyx* and *rubricalyx* "Afterglow" give progenies consisting of *rubricalyx* and *latifrons*. The theoretical expectation in each of these four cases involves a 2:1 ratio, which, however, is almost never closely approximated in actual experience. This general failure to yield a 2:1 ratio shows that other factors are also involved, including perhaps inequality in the successful formation of the different kinds of gametes, selective fertilization, and differential survival value of the zygotes.

These four mutations with characteristically splitting progenies are known as "half-mutants," a term originally used by de Vries (1918) with a somewhat broader significance, as he applied it to the result of the union of any newly mutated gamete with an unmutated gamete of the parent type, and assumed that this phenomenon is of necessity involved in the origin of almost every mutant type. More properly the four mutant types here under consideration might be designated *permanent half-mutants*, since most of the mutants to which de Vries applied the concept of "half-mutants" change their status in time from half-mutants to full mutants, while these four maintain their "half-mutant" condition permanently, owing to action of the one remaining lethal factor.

The present paper deals only with *Oenothera mut. erythrina*, presents two new kinds of genetic behavior, and describes seven striking new mutational segregations which have appeared within the past six years in my cultures of *Oe. mut. erythrina*.

HISTORICAL

None of the four permanent half-mutants now known was recognized as a half-mutant at the time of its first discovery. The *Oe. mut. rubri-*

nervis has been from the beginning of the experimental cultures of *Oenothera* one of the easiest to recognize. According to de Vries's account it was first observed by him in 1889 as an aberrant offspring in a culture of self-fertilized *Oe. mut. laevifolia*. As a derivative directly from *Lamarckiana* it first appeared as a single individual in 1890-91 in cultures comprising somewhat more than 10,000 plants of *Oe. Lamarckiana*, and during the next three years he found 31 *rubrinervis* plants among 23,800 plants of *Lamarckiana* and 733 other recognized mutants tabulated under the names, *gigas*, *albida*, *oblonga*, *nanella*, *lata* and *scintillans*. He first began to study the breeding behavior of *Oe. mut. rubrinervis* in 1895 and grew somewhat over 1000 offspring from selfed *rubrinervis* in each of several succeeding years. He overlooked the regularly recurring segregate, *Oe. seg. deserens*, and concluded that *Oe. mut. rubrinervis* was a fully constant elementary species. The first account of these studies was published in 1901 in *Die Mutationstheorie*, Vol. 1, pp. 155-163. Not until 1913 did de Vries note that *rubrinervis* regularly yields a progeny consisting of *rubrinervis* and *seg. deserens* (de Vries 1917).

The history of *Oe. mut. erythrina* is as follows. In 1905, at my request, Doctor de Vries sent me ten large rosettes of *Oenothera Lamarckiana*, collected in the same abandoned potato field near Hilversum, Holland, from which his original material of this species had been taken in 1886. These rosettes were received at the Carnegie Institution's Station for Experimental Evolution on April 7, 1905. In my culture 0557, produced by crossing two of these plants received from de Vries, one plant in a family of 77 was probably the first *Oe. mut. erythrina* ever seen by human eyes. It was noted in August 1906, when it was recorded as "*rubrinervis*." Several new specimens of the same type were observed the following year, and many have been noted in the *Lamarckiana* cultures derived from these ten wild rosettes during all the years which have since unrolled. They were always recorded as *rubrinervis* although it was soon noticed that they were in disagreement with de Vries's description of *rubrinervis* with respect to the brittleness of the branches. It is certain that the specimens noted in 1906 and subsequently were *mut. erythrina*, because the strain of *Oe. Lamarckiana* which originated from this new collection of wild rosettes has since been found to produce repeatedly and consistently only the tough-stemmed *Oe. mut. erythrina*, and has

never been known to produce the brittle-stemmed mut. *rubrinervis*. According to the statement of de Vries (1919), made when *erythrina* was first named and described, he found his first two specimens of this mutant in the summer of 1907 in the second generation of cultures from a large rosette which he set into his own garden at the same time that he shipped the above-mentioned ten rosettes to me.

From my first specimen of *Oe. mut. erythrina*, found in 1906, and from many new mutants of the same type which occurred in subsequent years from my cross-bred strain of *Lamarckiana* based on the 1905 shipment of rosettes, I have grown, over a period of three decades and more, hundreds of cultures from both self-fertilized and from cross-fertilized *erythrina* parents for comparison with the original strain of de Vries's *Oe. mut. rubrinervis* seeds of which had been received from de Vries on March 10, 1905. I continued this original *Oe. mut. rubrinervis* in my experimental cultures by repeated self-fertilizations while my *erythrina* cultures were being handled mainly as a cross-bred strain. When my cultures of *erythrina* were found to have tough stems while the de Vries strain of *Oe. mut. rubrinervis* had brittle stems, I naturally assumed that this difference was one of the effects of self-fertilization, as such, and I used as a descriptive differentiation the terms "selfed type" and "crossed type" of *rubrinervis* to indicate this difference in the toughness of the branches, not realizing that I was comparing two genotypically distinct types which owed their difference to their having originated as "parallel mutations" from two different strains of *Oe. Lamarckiana*, and that the latter were likewise genotypically differentiated in this ability to produce brittle-stemmed *versus* tough-stemmed half-mutants.

The two permanent half-mutants bearing the names *rubricalyx* and *rubricalyx* "Afterglow," were derived from *Oe. mut. rubrinervis* and never directly from *Oe. Lamarckiana*, in the cultures of R. R. Gates. The deep-red hypanthia resulted from a dominant gene-mutation which was discovered at Woods Hole, Massachusetts, in the summer of 1907, in an unguarded culture grown from mixed seeds from four specimens of *Oe. mut. rubrinervis*. The most notable difference between *Oe. mut. rubricalyx* and *Oe. mut. rubricalyx* "Afterglow," is the fact that the former has a circle of 6 chromosomes and 4 pairs, whereas the latter has a circle of 8 and only 3 pairs.

On the basis of Belling's (1927) brilliant observations and conclusions regarding chromosome circles in *Datura*, Darlington (1929), Cleland and Blakeslee (1930, 1931) and Cleland (1932, 1933) have plausibly explained the formation of circles of chromosomes in the *Oenotheras* as the result of segmental interchanges, that is, the exchange of ends by two non-homologous chromosomes. Darlington (1929, appendix) and Cleland and Blakeslee (1931) have shown how the permanent half-mutants, with circles of 6 or 8, may likewise be derived by segmental interchanges in a form like *Oe. Lamarckiana* which has a circle of 12 chromosomes and a pair. Cleland (1931) has shown that the circle of 8 of *Oe. mut. rubricalyx* "Afterglow" can be very simply derived from the circle of 6 of its parent *Oe. rubricalyx* Gates by the occurrence of a single additional segmental interchange and has also recently made a very thorough analysis of the different ways in which the half-mutant *erythrina* could be derived from *Oe. Lamarckiana* by a minimum of two coincident or successive segmental interchanges (Cleland 1942).

THE NORMAL PROGENY OF *Oe. mut. erythrina*

The recognition of the homozygous seg. *decipiens* as a regular and normal component of progenies of self-fertilized *erythrina* parents, was not clearly attained until the appearance of de Vries's (1919) paper in which the name *decipiens* was proposed, but the range of variation in each such progeny, to include both *erythrina* and *decipiens*, was noted very early, and such expressions as "dark *rubrinervis*" and "light *rubrinervis*" are found in my notes. But the dark (*decipiens*) and light (*erythrina*) variations were considered as merely the fluctuational extremes of a uniform biotype. Figure 1 shows a record of these extremes in a photographic plate made in 1910.

When *Oe. mut. erythrina* was finally understood to be a half-mutant, a meticulous effort was made to separate each progeny into its two components (a) mut. *erythrina*, the half-mutant parent type, and (b) the extracted homozygous seg. *decipiens*. It has been found that under favorable conditions this separation can be accomplished with a fair degree of success; but the conditions have rarely been so ideal that the grouping could be made with complete assurance of accuracy, and there has been usually a small amount of error in the classification, especially in the young rosettes.

From this it will be clear that the features which distinguish seg. *decipiens* from mut. *erythrina* are

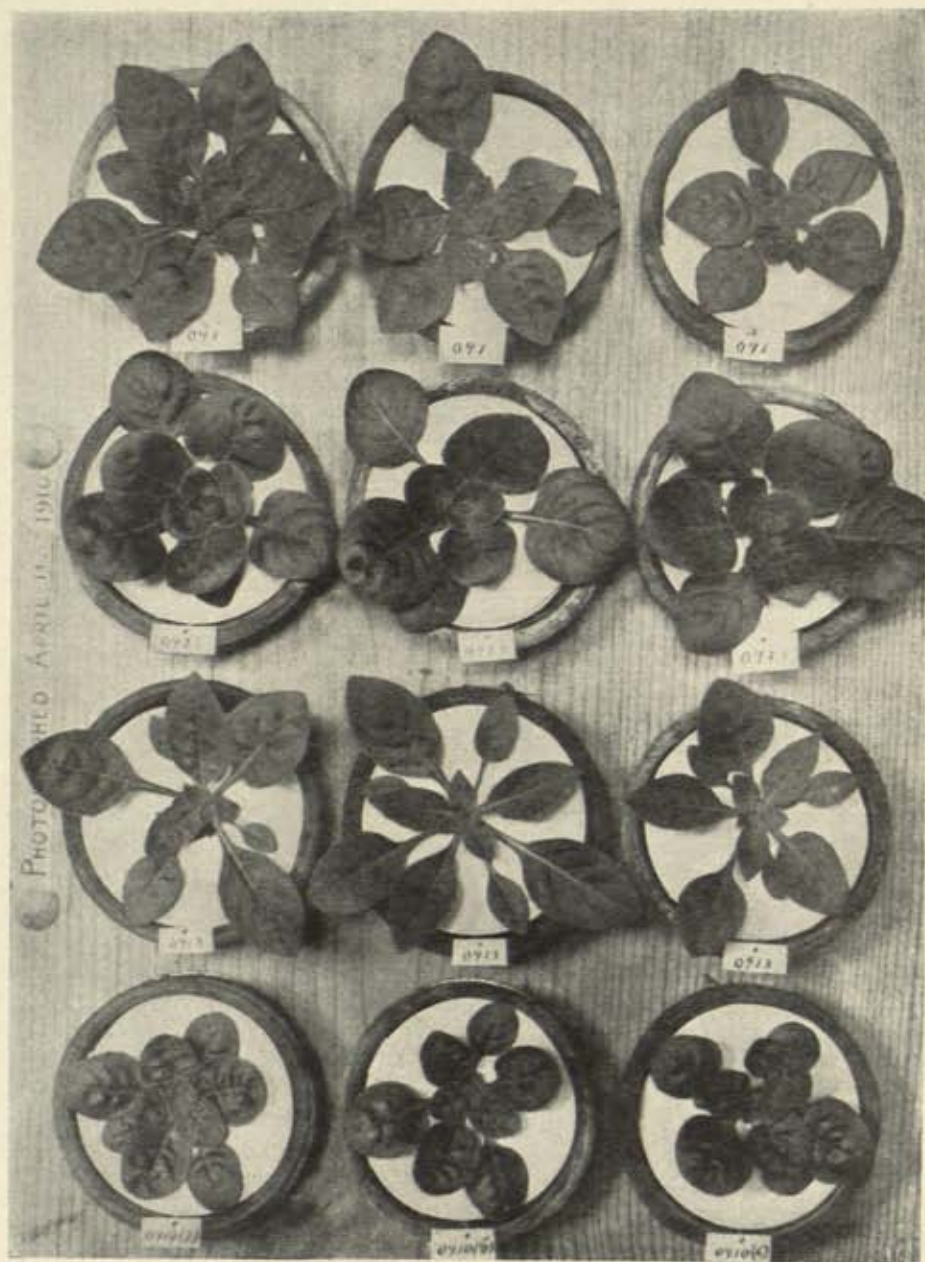


FIG. 1. Young rosettes of *Oe. Lamarckiana* (top row) and three of its chromosomal mutations, *gigas*, *erythrina* and *lata*. In this old photograph, taken by the writer on April 11, 1910, is shown very clearly the distinction between seg. *decipiens* (at left) and mut. *erythrina* nine years before seg. *decipiens* was reported by de Vries (1919) as a regularly recurring segregate.

neither sharp nor very conspicuous. As young rosettes which have grown well separated and under good environmental conditions seg. *decipiens* has slightly stiffer, darker green leaves with more noticeable and sharper denticulations on the margins of the younger leaves. Often the leaves are

slightly crinkled, relatively a little wider and a little sharper at the apex than in mut. *erythrina*. Seg. *decipiens* is usually of slower growth and maturity, its stems are usually rather irregularly crooked, the upper stem leaves likely to be again rather sharply denticulate, but this latter is like-

wise too variable to have much value as a diagnostic character. The bud-cones have less red pigment than in *erythrina*, and the pigmentation is less evenly distributed.

As a breeder seg. *decipiens* is greatly inferior to mut. *erythrina*. It is slower in development, and often fails to mature as an annual, while mut. *erythrina* is one of the surest of annuals when the seeds are sown in the greenhouse in mid-winter. Seg. *decipiens* and the homozygous segregates from the other half-mutants usually have scanty pollen, and produce a much smaller quantity of seed than the corresponding half-mutants. The best explanation of this marked difference between the heterozygous half-mutants and their homozygous segregates appears to be that the advantages in favor of the half-mutants is a striking illustration of the effect of heterosis, and the conclusion seems justified that the peculiar chromosomal behavior in the *Oenotheras* has been favored by natural selection of the strikingly more vigorous and more prolific heterozygotes.

Oenothera MUT. *pollicata* AS A RECURRENT
SEGREGATE FROM MUT. *erythrina*

I have reported in a previous paper (Shull, 1937) that the remarkable new mutant type mut. *pollicata* characterized among other things by the interpolation of a solid portion of hypanthium between the distal end of the ovary and the proximal end of the style, was the first characteristic which has been found to affect the entire group of *decipiens* segregates while leaving the *erythrina* component of that same family unaffected. The full importance of this case was not at first recognized because the first examples of *Oe.* mut. *pollicata* were found as mutations from *Lamarckiana*, and most of my experiments with *pollicata* involved only such as were associated with both of the *Lamarckiana* lethals. Not until 1934 was *pollicata* found associated with *erythrina* and as reported (Shull, 1937) there were in that year, three families each derived from a self-fertilized *erythrina*, in which all of the 117 *decipiens* plants which bloomed were *decipiens pollicata*, while all but one of the *erythrina* plants (286:1) in the same families were non-*pollicata*. This apparent replacement of *decipiens* with *decipiens pollicata* excited interest at the time only as giving additional proof that the *pollicata* gene is in the first linkage group where it is associated, in *Lamarckiana*, with the balanced lethals l_1 , l_2 , and in *erythrina* with only one of these, either l_1 or l_2 .

Sensing the possibility that I might have overlooked previous occurrences of *pollicata* when associated with *decipiens*, because of the late and poor development of the *decipiens* component of each *erythrina* progeny, I sowed in 1935 a new lot of seeds of the original *erythrina* mutant which appeared in 1930 in *Lamarckiana* family 2930. This new family from the old seed bore the number 34212 and duplicated family 30231 in which latter I would have had my first opportunity to overlook the *pollicata* character if it were actually present in 1931 in the *decipiens* component of a family ancestral to those families which in 1934 were found to contain seg. *decipiens pollicata*. Family 30231 had had 97 or 98 *decipiens* and 89 or 88 *erythrina*; 55 of the *decipiens* plants bloomed, but were not recognized as *pollicata*. However, when special attention was given to this point in family 34212, grown from the same seed in 1935, it was found that the family consisted of 59 *decipiens* and 66 *erythrina* and that 46 *decipiens* (all that bloomed) were *decipiens pollicata*, while the 59 *erythrina* plants which bloomed were all normal-styled, i.e., non-*pollicata*. This shows that seg. *decipiens pollicata* was present but unrecognized in my cultures in 1931, a year before mut. *pollicata* was first doubtfully discovered in 1932 in a *Lamarckiana* family and three years before it was actually recognized as a segregated component of an *erythrina* family.

The replacement of the entire group of *decipiens* plants in these families by *decipiens pollicata* presents no difficulty of interpretation, since the characteristic vegetative peculiarities of seg. *decipiens* are not notably changed by the presence of the *pollicata* gene. One needs only to think of the gene for tubular hypanthium and normal long stiff style being replaced by its mutational allele, the *pollicata* gene. But the other new types which have replaced seg. *decipiens*, or which have been added to the *decipiens* segregate in families from selfed *erythrina*, as presented below, do not suggest such a simple interpretation for them.

Oenothera seg. *petiolaris*, seg. nov.

The first and one of the most remarkable new mutational segregates I have found was discovered March 8, 1935, when family 3485 was potted from the seedpan to 75 mm pots. It could have been observed much sooner for we have found since that seg. *petiolaris* becomes sharply distinguishable from both *erythrina* and seg. *decipiens* in a very early seedling stage. Figure 2 shows a por-



FIG. 2. Seedpan 37457 with seedlings from a self-fertilized *Oe. mut. erythrina*, showing segregation of *seg. decipiens* and the first of the new segregations, *seg. petiolaris*. Photo April 1, 1938.

tion of a seedpan containing *mut. erythrina*, *seg. decipiens* and *seg. petiolaris*. The contrast becomes greater as the plants continue to grow. Every feature of the *petiolaris* plants is in striking contrast with the corresponding feature of the parent *erythrina*. The full grown rosette is gray

green, very coriaceous, and the leaves consist of very long petioles, and the very small blades are asymmetrical and variously and irregularly lobed, as shown in Fig. 3. *Seg. petiolaris* is a fairly hardy type and withstands field conditions well, but it is of relatively slow growth, as might be

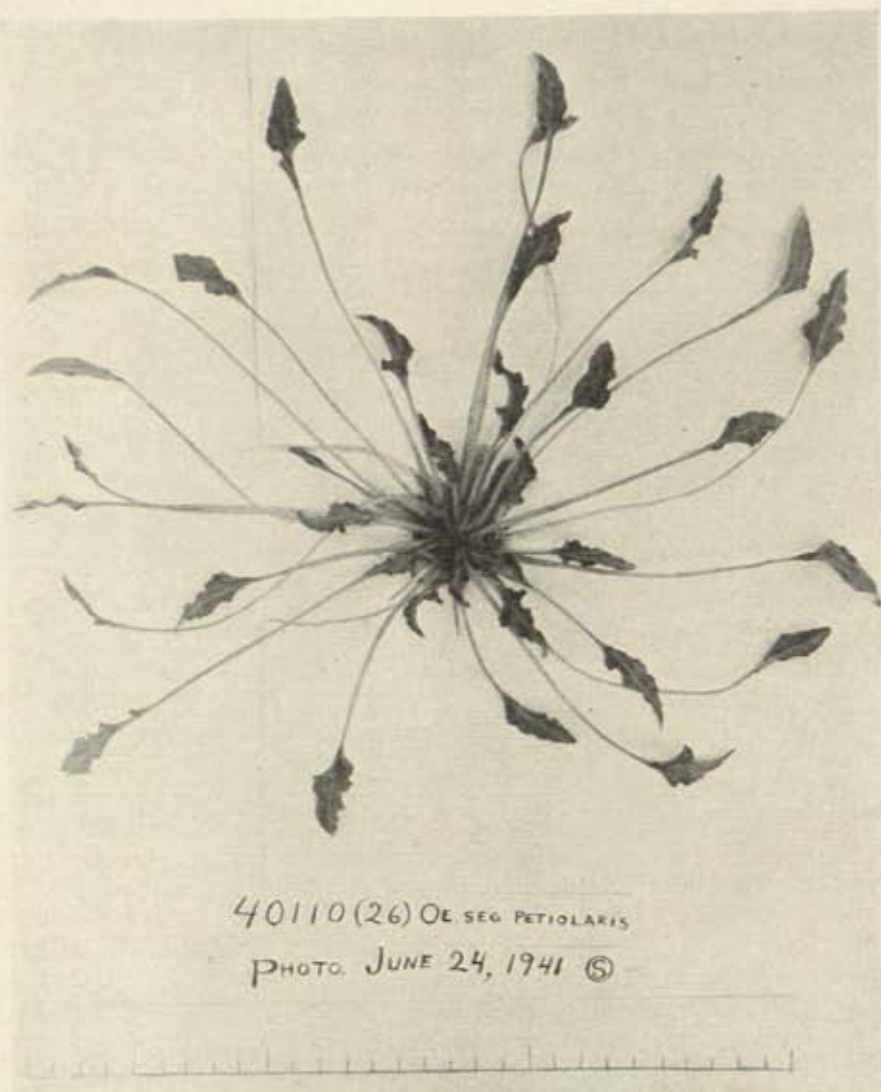


FIG. 3. Rosette of *Oe. seg. petiolaris* six weeks after being set in the experimental field. The smallest segments of the scale below are centimeters.

anticipated because of the small volume of the green tissues.

Under most favorable field conditions a few of the plants produce stems well branched, the branches notably straighter than in *decipiens* and more erect than in *erythrina* (cf. Figs. 4 and 5). More commonly no basal branches develop, but very numerous short branches develop on the central axis. The stem leaves are very numerous, narrow, with upturned nearly entire margins and much shorter petioles than in the rosette leaves, but still much longer than in *erythrina* stem leaves. The petioles of the stem leaves of *seg. petiolaris* are one-third to one-half as long as the blades

(see Fig. 29). A very few *petiolaris* plants have come to bloom in the field, but rarely early enough to be successfully used in breeding. In this first family (3485) which contained *seg. petiolaris* only one of the 43 *petiolaris* plants matured early enough to be bred. Numerous flower buds began forming on this most precocious *petiolaris* plant about the end of July, but for a long time these buds were regularly dropped long before they reached full development. Not until the end of August were some buds retained until they reached the flowering stage. The buds and the petals of *seg. petiolaris* are notably unlike any I have seen in any other type of *Oenothera*. The calyx con-

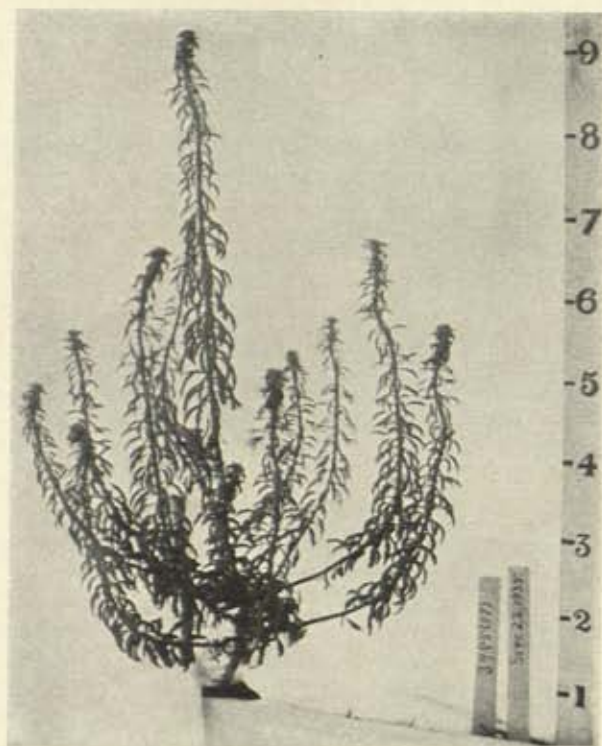


FIG. 4. *Oenothera* seg. *petiolaris*, showing characteristic stem-leaves and a rather unusual branching habit.

sists of narrow sepals which cohere persistently at their tips, but begin to separate from each other in the mid-region of the bud-cones even while the buds are extremely small, thus forming a 4-barred cage within which the other floral parts develop. Sometimes the pressure of these interior organs of the flower succeed in separating one or two or even all four of the sepals, but quite commonly the petals and some of the stamens protrude between the bars of the cage formed by the permanent apical coherence of the sepals (Figs. 6 and 8). These sepals are strap-shaped proximally, but distally the edges are inrolled and occasionally grip an anther securely in this convolute portion, and hold it even when the sepal has been separated at the tip from its fellows. The petals are narrow, especially in their proximal half or more, where they are rendered stiff by a backward (downward) fold along their median line (Figs. 6-8). The cross-section of this proximal portion of the petal has the form of an inverted V or the printer's caret. Distally the petal is broadened and spreads laterally and is irregular in distal outline, corresponding in some degree with the irregular outline of the leaf blades.

The anthers are well developed but usually almost or quite devoid of pollen. I did find good pollen in several anthers of this first sexually matured specimen of seg. *petiolaris* and succeeded in getting a few good capsules from controlled pollinations. The hypanthia of seg. *petiolaris* are relatively long, hollow throughout, and traversed by the rather heavy style which is rendered crooked distally by its imprisonment within the cage formed by the cohering sepals. The stigmas were heavy, clumsy and somewhat irregular.

In 1936 I grew one family (35240) of 41 plants from self-fertilized seg. *petiolaris*. Of these 41 plants, one was *decipiens*, and one a modified *petiolaris* which had no clear-cut blades, but consisted of petioles merely slightly expanded distally. All the rest were like their self-fertilized parent, typical seg. *petiolaris*, as above described, but none of these bloomed early enough to be used for a continuation of the experiment.

Another family (35241) consisting of 37 plants resulted from the pollination of seg. *petiolaris* with pollen of a seg. *decipiens* sib. When making this cross I was entertaining the working hypothesis that the *petiolaris* would be found to bear the same relation to the *velans* complex and its lethal, l_2 , that *decipiens* seemed to have to the *gaudens* complex and its accompanying lethal, l_1 , a hypothesis that has not been substantiated by



FIG. 5. Habit of *Oe. mut. erythrina*, for comparison with Fig. 4.



FIG. 6. A single opening flower of *Oe. seg. petiolaris* showing the petals escaping from the frame-work formed by the terminally cohering sepals. Photo in 1936 by W. H. Brittingham.

subsequent results. On this hypothesis it was anticipated that *petiolaris* \times *decipiens* might give a family of uniform *erythrina*, which could be expected subsequently to split regularly to *decipiens*, *erythrina* and *petiolaris* in about a 1:2:1 ratio. The 37 plants of family 35241 consisted of 17 *decipiens* and 20 probably *erythrina* of which latter 6 were smaller and slightly darker green, but believed to be *erythrina*, nevertheless.

The seg. *decipiens* plant used in the cross with seg. *petiolaris* was also selfed, and the progeny from this selfing was grown in 1936 as family 35242. This consisted of 152 plants of which 35 died in the pots after they were set from the seedpan. One plant was divergent from the rest, having narrower leaves with declining margins. All of the remaining 116 plants were seg. *decipiens*. In the experimental field 48 of these died, 23 failed to bloom, mostly remaining winter rosettes, and 54 which bloomed were all *decipiens pollicata*.

In the same family (3485) which contained the first plants of seg. *petiolaris*, I also self-pollinated five specimens of *Oe. mut. erythrina*, expecting in this way to insure the continuation of seg. *petiolaris* even though the meager results from the direct breeding with *petiolaris* itself should prove disappointing. The resulting families, 35243 to 35247, inclusive, gave seg. *petiolaris* again in three of the families, 35244, 35245, 35247, which produced jointly 153 *decipiens*, 186 *erythrina*, 91 *petiolaris*, and 24 not exactly identified. The other two families of this same parentage, 35243 and 35246, contained no *petiolaris*, but consisted jointly of 144 *decipiens*, 150 *erythrina* and 32 not exactly identified.

Finding that *Oe. seg. petiolaris* could not be depended on to supply breeding material until too late in the season, and then in only a few individuals, I decided in 1937 to try the effect of long-day treatment. To this end I brought well grown rosettes of several types, including seg. *petiolaris*, to the greenhouse before freezing weather set in in the field and suspended about 50 cm above them a 500 watt incandescent lamp and above this a bright sheet of tin-plate as a reflector. This lamp was lighted at dusk each evening from December 1, 1937, on, and turned off regularly about 10 P.M. The plants responded to this treatment by developing stems which grew well and formed vigorous flowering specimens in mid-winter (Figs. 7, 8). I thus secured scores of fully developed flowers of *Oe. seg. petiolaris* which had rarely produced more than two or three flowers on any plant in the field.

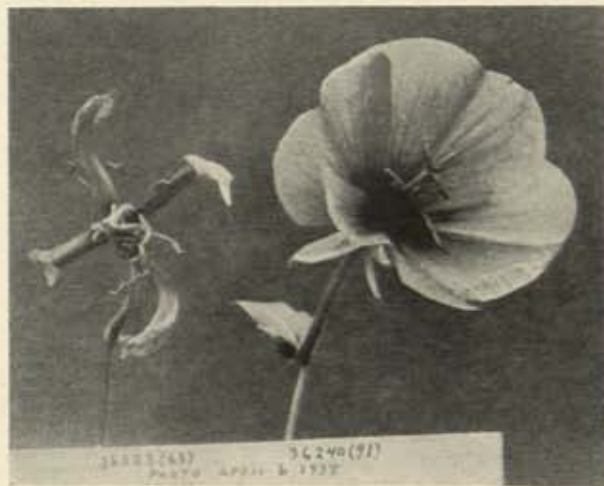


FIG. 7. A single flower of *Oe. seg. petiolaris* compared with a flower of *Oe. Lamarckiana*. The latter is practically indistinguishable from a flower of *Oe. mut. erythrina*.



FIG. 8. A portion of an inflorescence of *Oe. seg. petiolaris* 36323(63), brought to full maturity by long-day treatment. Photo April 6, 1938.

In all details these flowers agreed with those produced naturally in the field, but unfortunately for my breeding program they were practically pollen sterile. I did succeed in getting several small capsules by applying pollen from *Lamarckiana rubrifolia* which was also receiving long-day treatment at the time, to the stigmas of *petiolaris*. These capsules contained 25 seeds which were sown on February 8, 1939, under the family number 38246, and produced 13 plants, all of which seemed to be *Lamarckiana rubrifolia*, though several of the smaller plants had the red pigmentation on the rosette leaves more broken and patchy than in their more vigorous sibs. There was thus a

practically complete dominance in the F_1 of the paternal characteristics over the numerous peculiarities of *seg. petiolaris*.

Two families of the current year (1941) resulted from selfing two of these F_1 plants in family 38246. These two families 4098 and 4099, representing the F_2 of *petiolaris* \times *Lamarckiana rubrifolia*, present a series of puzzling genetical problems.

Family 4098 from a patchy *Lamarckiana rubrifolia* parent consisted of 115 plants (from 300 seeds), only one of which approximated *petiolaris* by having the leaves reduced to petioles without conspicuous blades. All the rest were *Lamarcki-*

TABLE 1¹PROGENIES CONTAINING *Oe. seg. petiolaris*, FROM SELF-FERTILIZED *Oe. mut. erythrina* SIBS OF *petiolaris*

Grandparent Number	Parent Number	<i>Decipiens</i>	<i>Erythrina</i>	<i>Petiolaris</i>	Other variants or doubtful
3351	3485	53	63	43	4
	35239	34	49	33	1
3485	35244	47	56	33	23*
	35245	42	46	26	4
	35247	64	69	32	12*
35239	36297	66	92	51	—
	36298	44	63	42	6
	36299	0	89	29	—†
	36300	42	63	29	—
36329
	37466	73	48	44	3
	37467	54	100	59	—
	37468	47	71	47	—
37434
	38513	64	88	57	—
	38515	47	107	54	—
	38516	18	56	28	109‡
	38517	58	109	48	—
	38520	12	23	16	—
	38529	29	47	36	23§
38516	38530	51	147	66	—

	39497	62	61	33	6
	39499	43	36	26	—
	39502	11	25	6	14**
	39504	3	26	11	19**
38296	39508	2	8	2	—
	39509	12	22	8	2
	39511	9	21	9	—

39497
	40106	13	30	9	—
	40108	16	28	8	—
	40110	0	56	18	10††
	40111	13	27	14	1
	40113	31	38	30	4
Totals (159 families)	40114	18	37	15	1

¹ This table is abbreviated by the omission of 127 entries, including none in which mutational segregations seem to have been present. The complete table is issued through Auxiliary Publication, and may be obtained from the non-profit Bibliofilm Service, American Documentation Institute, 2101 Constitution Avenue, Washington, D. C., by ordering Document No. 1601, remitting 30 cents for copy in microfilm, readably enlarged full-size on reading

ana rubrifolia(—) having the same defective pigmentation that characterized the parent, and implying that this patchiness of the pigmentation was genotypically determined. Thirty-two of the plants differed from the rest only in being relatively depauperate. A considerable number of the plants of this family had the young rosettes raised more or less above the ground on naked stems, 1–3 cm long.

Family 4099 is in striking contrast with 4098, for out of 185 plants secured from sowing 300 seeds only 15 were *Lamarckiana*-like, and 170 *petiolaris*. All of the former were *rubrifolia*, while none of the *petiolaris* showed any indication of *rubrifolia* pigmentation. The near disappearance of *Lamarckiana rubrifolia* in family 4099 and the all but complete disappearance of *petiolaris* in 4098, are notable features of these two F₂ families, since *petiolaris* is recognized as a recessive type. The explanation is presumably inherent in the distribution of the lethal factors possessed by the given parents.

That *Oe. seg. petiolaris* is not an alethal form, as I at first supposed, seems to be demonstrated by this result. I believe that such a hypothesis is rendered untenable also by the fact that *seg. petiolaris* has a circle of six and four pairs of chromosomes² exactly as in *erythrina*, not the seven pairs that would be expected in an alethal form which balanced the seven-paired *seg. decipiens*.

The unsatisfactory breeding potentialities of *Oe. seg. petiolaris* have led me to concentrate on the use of *erythrina* sibs for a continuation of my

² I am indebted to Dr. D. G. Catcheside of Cambridge University, England, for this determination. Dr. Catcheside visited my cultures on August 22, 1937 and finding a plant of *seg. petiolaris* in bud took material for a smear. He reported the result the following day.

machine or hand viewer, or \$1.00 for copy in form of paper photoprints readable without mechanical aid.

* These were smaller, darker green rosettes of unknown identity, probably a new mutational segregate.

† In this family *Oe. seg. petiolaris* appears to have replaced *seg. decipiens*, but as this is the only family in which this has been the case, it seems more likely that the *decipiens* is replaced here by *seg. sublethalis*, as discussed later in this paper.

‡ Of this group of 109 plants, 108 are assumed to have been *Oe. seg. diminua*, discussed in a later section of this paper.

§ These 23 were of *erythrina* form but definitely smaller, probably an unidentified mutational segregate.

** These were *Oe. seg. diminua*.

†† These ten plants were the new *Oe. seg. elongata* which is discussed in a later section.

studies of this new segregant, and particularly in studying the different types of families produced by this strain of *Oe. mut. erythrina*. These extensive breeding tests of many different individ-

uals of *Oe. mut. erythrina* have led to the discovery of the other remarkable mutational segregations which are described in this paper. It is to be remembered, in what follows, that the several *erythrina* plants whose progenies are included in the tables and which have differed from one another genetically in various characteristic ways, have been quite indistinguishable from each other

TABLE 2¹

PROGENIES CONTAINING NO SEG. *petiolaris*, FROM SELF-FERTILIZED *Oe. mut. erythrina* SIBS OF *petiolaris*

Grandparent Number	Parent Number	<i>Decipiens</i>	<i>Erythrina</i>	Other variants or doubtful
3351	3484	45	74	4
3484	35243	82	86	15*
3485	35246	58	68	17*
35239	36296	83	104	—
	36302	47	82	2
	36303	56	51	4
	36304	2	85	—†
	36306	70	64	—
	36308	70	81	2

36329	37462	62	109	—
	37464	66	114	1
	37467 ^{1/2}	69	111	—
37414	38294	71	87	2
	38295	51	124	—
	38297	69	88	2
37419	38499	71	106	—
	38500	49	88	—

38300	39519	72	117	—
	39523	80	99	—
	39528	50	115	—
	39530	1	86	3†
39497	40103	31	47	—
	40104	32	52	—
	40105	36	70	—
	40107	32	78	—
	40109	50	53	—

Totals (109 families)		5625	10181	124

* Probably unidentified mutational segregations.

† In these two families seg. *decipiens* is assumed to be nearly or quite eliminated by an exchange with seg. *sublethalis* as discussed in a later section.

¹ This table is abbreviated by the omission of 83 entries, including none in which mutational segregations seem to have been present. The complete table is filed with the American Documentation Institute, Washington D. C. See footnote to Table 1.

TABLE 3

PROGENIES FROM SELF-FERTILIZED *Oe. mut. erythrina* IN FAMILIES WHICH CONTAINED NO SEG. *petiolaris*, THAT IS, FROM FAMILIES LISTED IN TABLE 2

Grandparent Number	Parent Number	<i>Decipiens</i>	<i>Erythrina</i>	Other variants or doubtful
36321	37422	56	106	—
	37423	47	98	—
	37424	35	80	—
	37425	70	127	—
	37426	42	94	—
	37427	31	75	1
	37428	0	61	40*
	37429	31	84	—
	37430	21	61	—
	37431	19	47	—
36328	37446	16	44	1
	37447	31	43	—
	37448	70	92	3
	37449	67	116	1
	37450	69	139	1
	37451	56	119	3
	37452	81	101	2
	37453	39	90	2
	37454	52	68	—
	37455	71	115	—
	37456	73	127	—
Totals (20 families)		977	1826	14

* These 40 plants were *Oe. seg. contracta* which replaced *Oe. seg. decipiens* in this family as will be recounted in the next section of this paper. This family is not included in the totals at the bottom of the table.

phenotypically; also that all the breeding has been by completely hand-controlled self-fertilizations. Most of the families from *erythrina* sibs of seg. *petiolaris* are assembled for record and study in Tables 1 and 2, but a few appear incidentally in subsequent tables. Only samples of Tables 1 and 2 are presented here. The complete tables are issued through Auxiliary Publication and is obtainable by purchase at cost from the American Documentation Institute, Washington, D. C. The other tables are published here in full. In Table 1 are given the progenies of *erythrina* sibs of *petiolaris* that showed *petiolaris* segregates, while

in Table 2 are the progenies of the same origin which produced no *petiolaris* segregates. By reference to the totals at the bottom of Table 1 it will be seen that 157 of the listed *erythrina* sibs of *petiolaris* have yielded progenies consisting of the three main categories, *decipiens*, *erythrina* and *petiolaris*, while Table 2 shows that in 109 families of corresponding origin the main categories are only the two already familiar ones, *erythrina* and *decipiens*. From this it appears that the *erythrina* sibs of seg. *petiolaris* are, in nearly equal numbers, of two kinds with respect to their ability to segregate out a group of *petiolaris* plants in their offspring.

When we breed the *erythrina* plants in the families of Table 2, which contained no *petiolaris*, we find that the ability to produce *petiolaris* has apparently completely disappeared, as may be noted in Table 3, in which 20 such progenies are given. In this group of twenty families there was an exceptionally close approximation to the 1:2 ratio of *decipiens* and *erythrina*. There were 54 aberrant or doubtful individuals, but not one of these showed any resemblance to seg. *petiolaris*. In other words there seems to be a perfect segregation of the ability of mut. *erythrina* to segregate a class of *petiolaris*.

Oenothera seg. *contracta*, seg. nov.

The next example of unexpected mutational segregation from *Oe. mut. erythrina* was discovered March 20, 1938, in a seedpan bearing the family number 37428. The plants in this pan were about three weeks old, but were easily distinguished as belonging to two strongly contrasted phenotypes, of which one was apparently *erythrina*, the other a much smaller remarkably dark green, heavily crinkled, shining form which was at once named *Oe. seg. contracta* (Fig. 9). This family appears in the first section of Table 3, where all of the tested sibs of its parent are recorded. It was notable because its progeny consisted of 61 *erythrina* and 40 seg. *contracta*, instead of splitting in a 2:1 ratio of *erythrina* and seg. *decipiens*. In other words, seg. *contracta* has completely replaced seg. *decipiens* in this family. Figure 10 shows the two phenotypes present in this family and Fig. 11 allows a comparison of the new seg. *contracta* and the seg. *decipiens* which seg. *contracta* has displaced.

The plants of seg. *contracta* are very hardy and there are practically no losses in the seedpan nor in pots in the greenhouse, but they are of slow



FIG. 9. Portion of seedpan 37428 containing *Oe. mut. erythrina* and the first appearance of *Oe. seg. contracta*, about three weeks after germination. No seg. *decipiens* occurs in this culture. Photo March 20, 1938.

growth and notably smaller than *erythrina* or seg. *decipiens* of the same age. They also withstand well being reset to the field, but have never begun to form stems in the field. The seg. *contracta* plants in family 37428 began to die after they had grown for some time in the field, and by mid-August all had died. I was not greatly concerned over their loss, since it was obvious that they would never proceed beyond the rosette stage. Because of their obvious replacement of seg. *decipiens* in this family, I predicted that every *erythrina* plant in this family, if selfed, would give seg. *contracta* and mut. *erythrina* again in about the ratios which would otherwise have been presented by seg. *decipiens* and mut. *erythrina*.

To test the validity of this assumption I self-pollinated eleven *erythrina* sibs of these first seg. *contracta* plants and grew the resulting progenies in 1939. The record of one of these families (38314) was unaccountably lost. The remaining ten families, with eleven progenies grown from similar parentage in 1940, are presented together

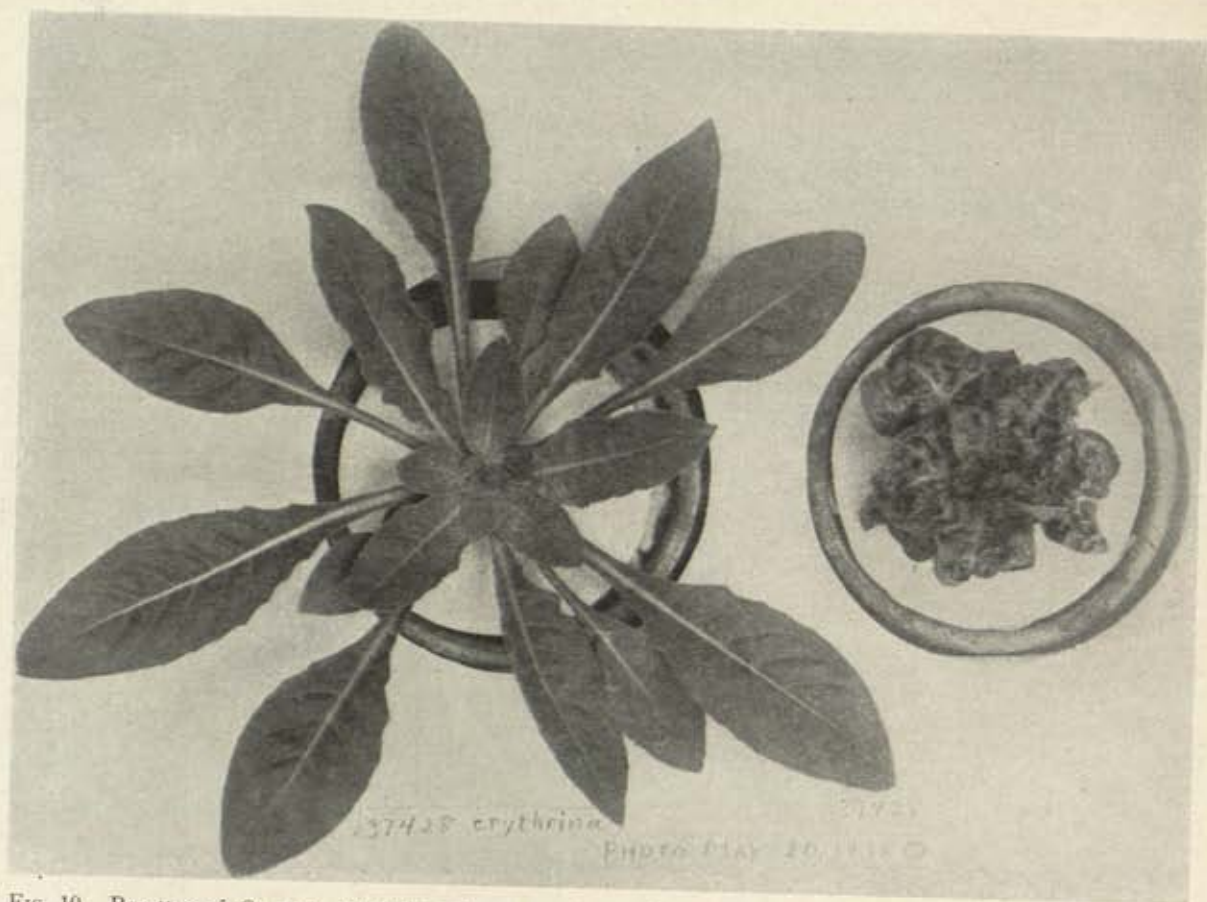


FIG. 10. Rosettes of *Oe. mut. erythrina* and *seg. contracta*, the only two types occurring in family 37428. Photo May 20, 1938.

with the original family 37428, in Table 4, where it is seen that every one of these *erythrina* parents produced the expected segregation of *erythrina* and *seg. contracta*, with a considerable excess of *contracta* over the one-third theoretically expected. This excess accords with the excess of *seg. decipiens* commonly found in the progenies of the original normal *mut. erythrina*. A notable feature of the families in this table is that in each of two of these families, 39536 and 39540, there was a single specimen of typical *seg. decipiens*. These two families taken together consisted of 80 *contracta*, 160 *erythrina* and 2 *decipiens*. Since *seg. contracta* has replaced *seg. decipiens*, these two *decipiens* plants suggest the possible occurrence of reverse mutation. Such a suggestion may be borne in mind in other cases where *seg. decipiens* has unexpectedly reappeared.

Two of the families in Table 4 are unique in having each a third segregated group in addition to *mut. erythrina* and *seg. contracta*. Family

39531 had in addition to 59 *contracta* and 66 *erythrina*, a group of 24 plants described as "darker and smaller than *erythrina*, but velvety, slightly crinkled, with repand denticulations." This group represents undoubtedly a new mutational segregation, but inadequate attention was given to these plants, and consequently their identity remains in doubt. The other family, 39533, had besides 25 *seg. contracta* and 61 *mut. erythrina*, a group of 16 *Oe. seg. cyanea* which will be discussed in the next section of this paper.

As stated above, all the *contracta* plants in the original family 37428 had died by mid-summer of 1938. The same result was experienced in the *contracta*-containing families in 1939, so that it was impossible to use long-day treatment to promote their maturation, which I had found effective in the case of *seg. petiolaris* and in some other retarded forms. Steps were taken in 1940 to keep *contracta* plants alive, if possible, for a longer time. To this end the *contracta* group of family

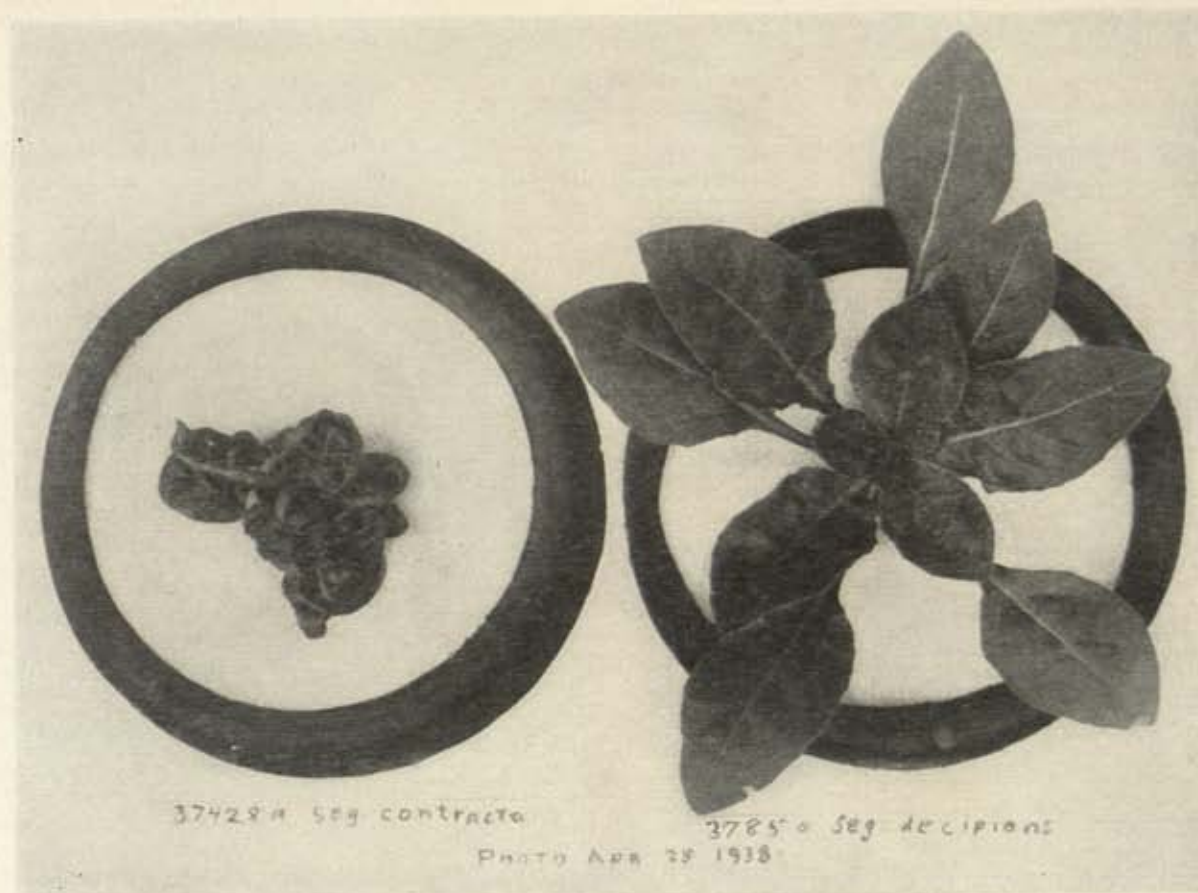


FIG. 11. Young rosette of *Oe. seg. contracta* (37428) and *Oe. seg. decipiens* (3785), the form which *seg. contracta* replaced in culture 37428. Photo April 25, 1938.

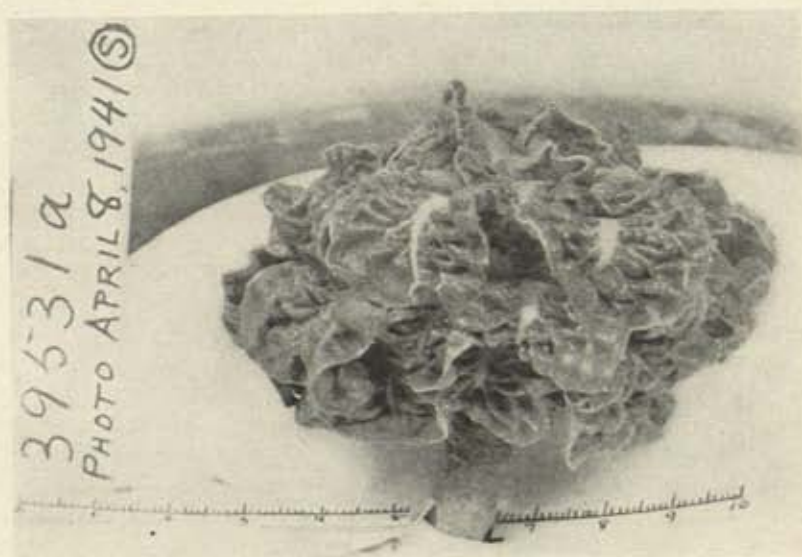


FIG. 12. A rosette of *Oe. seg. contracta* (39531), thirteen months old, which received long-day treatment daily from November 1940 to April 1941. Photo April 8, 1941.

TABLE 4
PROGENIES OF SELF-FERTILIZED *Oe. mut. erythrina*
IN WHICH SEG. *decipiens* HAS BEEN REPLACED
BY SEG. *contracta*

Grandparent Number	Parent Number	<i>Contracta</i>	<i>Erythrina</i>	Other variants or doubtful
36321	37428	40	61	—
37428	38304	108	77	—
	38305	102	93	3
	38306	128	110	—
	38307	108	80	—
	38308	87	84	1
	38309	96	100	—
	38310	97	103	—
	38311	90	98	—
	38312	52	72	—
	38313	83	98	—
38305	39531	59	66	27*
	39532	39	87	—
	39533	25	61	20†
	39534	41	96	—
	39535	31	69	3
	39536	54	74	1
	39537	51	88	1
	39538	66	72	1
	39539	47	71	6
	39540	49	90	1
	39541	17	45	—
Totals (22 families)		1470	1795	64

* 24 of these were of a new undescribed mutational segregation.

† 16 of these were *Oe. seg. cyanea*, as described in a later section of this paper.

39531 was not set to the field, but the plants were given various treatments in or near the greenhouse where they could be under constant observation and given needed attention to prevent injury from drought or other unfavorable conditions. One group, set in a bed of earth in the greenhouse, were soon eliminated by fungus disease, but of 8 plants set in large pots and sunk in a flower-bed near the greenhouse one survived until fall and passed the winter in good health under long-day treatment, but showed no inclination to run up a flowering stem. As new leaves formed above, the old leaves disappeared below, thus resulting in a maximum-sized rosette borne at the top of a very slowly elongating heavy stem (Fig. 12).

Another group of 32 of these *contracta* plants was set in a coldframe and protected by a lattice-work screen from too effective action of the sun. Many of these continued to grow slowly during

the summer, and greatly to my surprise, five which over-wintered in the coldframe, began quite early in the spring of 1941 to form stems. All of these have continued to grow and have developed stems from 60 to 80 cm tall (Fig. 13). It will be noted that there are no basal branches but some branching toward the tops of the main axes. Early in

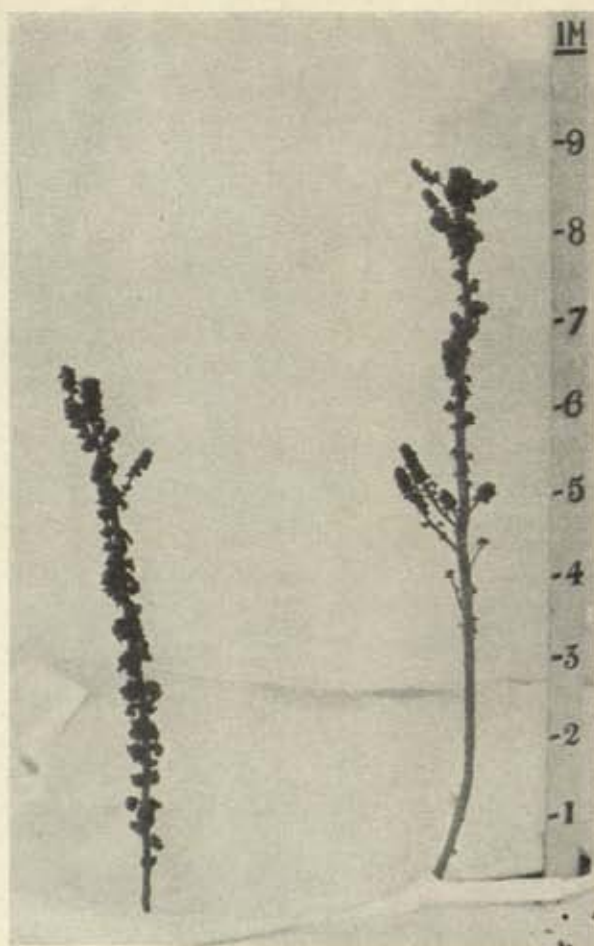


FIG. 13. Habit of mature *Oe. seg. contracta* (39531), sixteen months old. These wintered in a coldframe but were not given artificial lighting. Photo July 15, 1941. Compare with habit of *Oe. mut. erythrina* shown in Fig. 5.

July, 1941, several of them began to show bud-tips on the knoblike ends of the stems. The growth of these proceeded very slowly and it was fascinating to see a few of these buds enlarge, then show the development of the characteristic *erythrina* pigmentation on the bud-cones. But it was very disappointing to find that these enlarging buds had been induced to develop, only by the development within each of them of a larva of

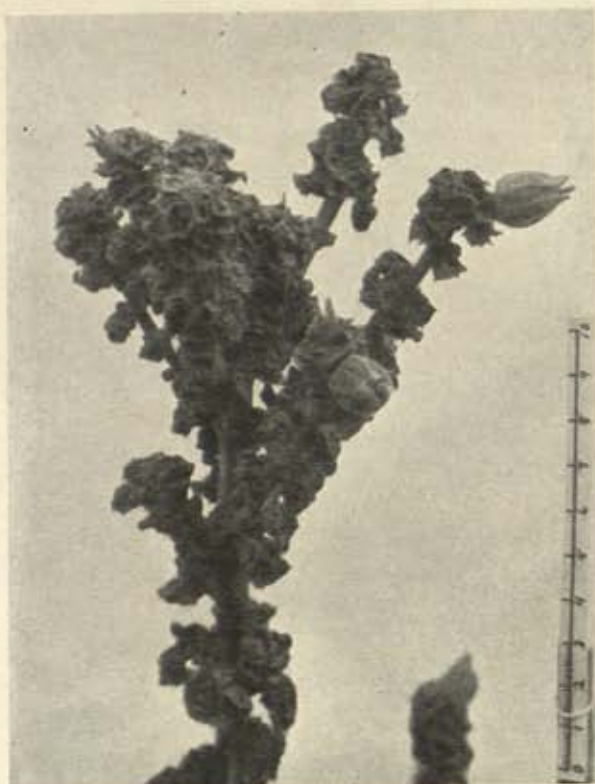


FIG. 14. *Oenothera seg. contracta* inflorescence with bud-galls produced by *Mompha stellella* Busck. Photo July 18, 1941.

Mompha stellella Busck, an insect which produces familiar bud-galls on other species of *Oenothera*, as described long ago by Gates (1910), and well known to all American growers of *Oenothera* cultures. A growing doubt that normal buds would be produced by these plants led to a more careful study of these galls than otherwise would have seemed necessary. The remarkable bud-cones of these galled buds reach a size of 12 mm long not including the free tips and 12 mm wide, and the heavy well-separated free tips were 4-5 mm long (Fig. 14). It was recognized that the form and size of these bud-galls would give little hint as to the form and dimensions which would be seen in normal buds of *Oe. seg. contracta*, should these ever develop. They differ from the corresponding bud-galls of *Oe. mut. erythrina*, *Lamarckiana*, etc., in remaining closed or only with an insignificant split between the sepals in the proximal portion of the cone where bud-galls of other forms split widely thus conspicuously displaying the petals. The bud-galls of *seg. contracta* are thus short barrel-shaped or cylindrical instead of roughly cone-shaped as in other forms. When the calyx

is removed the corolla is seen to be tightly packed and very crumpled, with a thickened inward fold along the median line of each petal. The essential organs of the flower are completely ruined by the intruder, the style and stigmas being eaten out and the filaments of the stamens abnormally shortened and thickened, and anthers are missing or are flat disks of tissue scarcely recognizable as anthers. The hypanthium is reduced to a very short thick obconical structure which gives no hint as to whether the natural hypanthium will be *pollicata* or will have the normal tubular form. The presence or absence of a solid tubular form. The presence or absence of a solid tubular form is a very important question here, since *seg. contracta* has replaced *seg. decipiens pollicata*.

After watching the development of about a dozen of these bud-galls, while all the other buds seemed inclined to remain small four-pointed stars consisting of the widely divergent free tips, I

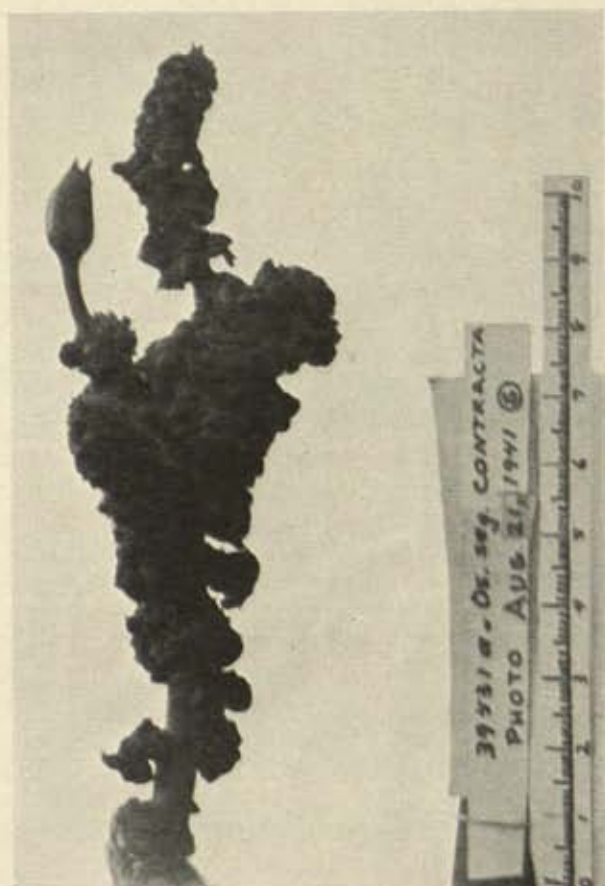


FIG. 15. *Oenothera seg. contracta* showing a normal bud on the day preceding anthesis. A very slight increase in diameter of the hypanthium marks the limit between solid and tubular part of the hypanthium. Photo August 21, 1941.

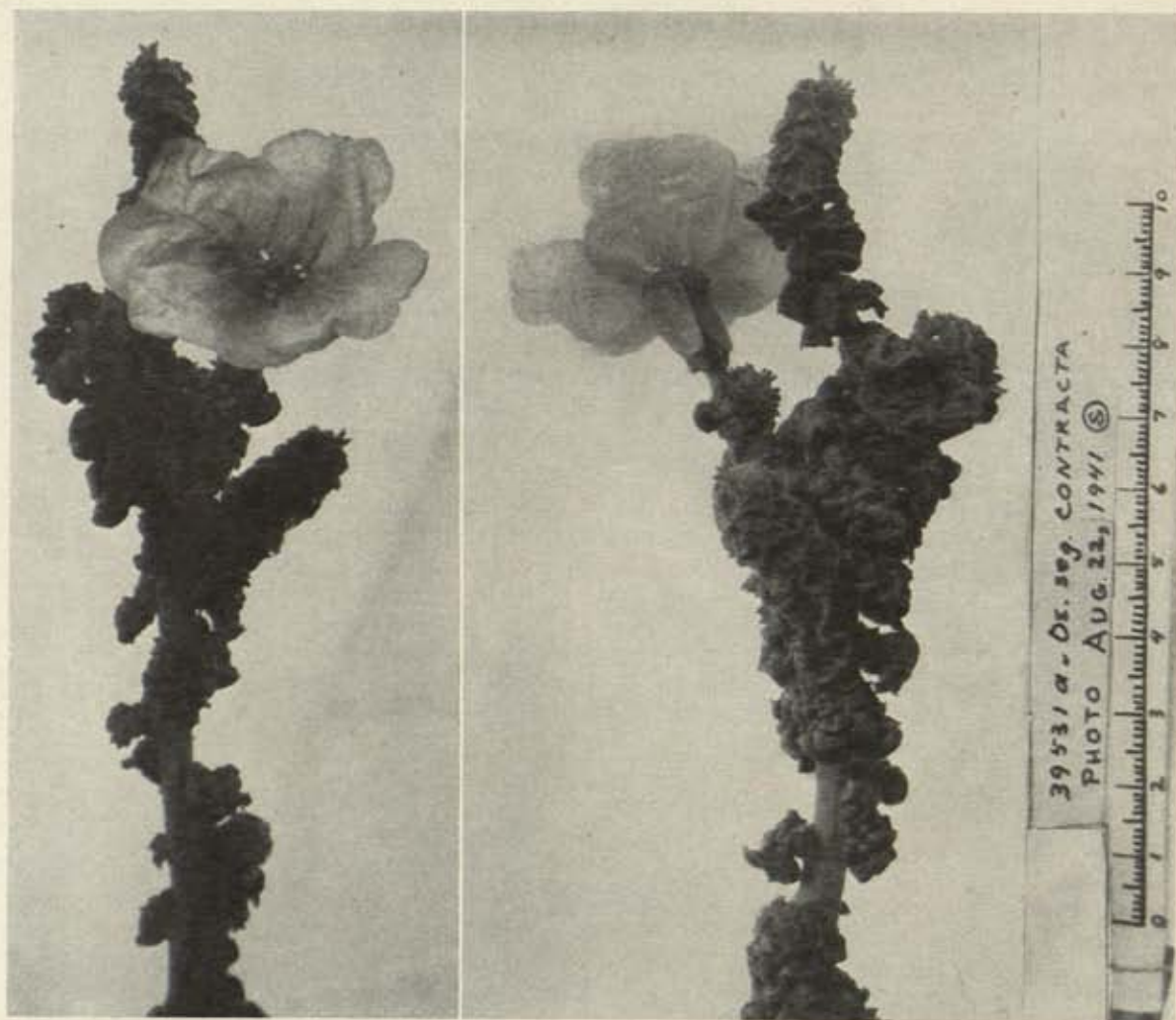


FIG. 16. A normal flower of *Oe. seg. contracta*. The rear view shows the broad short sepals nearly hiding the hypanthium.

surmised that no normal buds would be produced, and that the normal flowers of *seg. contracta* would remain forever unknown. In this I was happily mistaken, for about August 1 I noticed the enlargement of several buds which did not show the swollen flaring hypanthium of the Mompha galls, and I gradually became convinced that here at last normal buds were developing. These normal buds (Fig. 15) did not differ as much from the bud-galls, however, as I expected, the main differences being that the normal bud-cone does not attain as large size as the galls and is less intensely reddened, though showing the *erythrina* type of reddening on the cones. The fully developed bud on the day preceding anthesis had a hypanthium 10-15 mm long, topping an

ovary 5-6 mm long, and cones were about 10 mm long and 7-8 mm in diameter, the free tips 4 mm long, erect or slightly divergent. Approximately one-half of the hypanthium was solid, thus indicating that *seg. contracta* is *pollicata* like the *seg. decipiens* it has displaced.

The enlargement of these buds proceeded slowly, but finally the first flower opened on August 8, the second on August 11, a third on August 13 and a fourth on August 22, 1941 (Fig. 16). These flowers were on three different plants, but were all essentially uniform, except that the first one had a slightly blighted style and stigma and the flower as a whole was only three-fourths as large in diameter as the later healthy flowers (32 mm as compared with 44-45 mm). As com-

pared with *Oe. mut. erythrina*, a single petal of the latter would just cover the entire normal flower of seg. *contracta*. As anticipated the petals are notably wider than long, 25–28 mm wide and 18–22 mm long, and extremely crinkled. Occasionally a petal has one or two conspicuous notches in the distal margin. The anthers are crooked and usually devoid of pollen, but a small quantity of seemingly good pollen has been produced on the later flowers. The style and stigma are typical *pollicata*, the styles being limp and the stigmas heavy and clumsy, so that they decline in positions determined mainly by gravitation.

Oenothera seg. cyanea, seg. nov.

I have already mentioned, in the last section, two families which are entered in Table 4, but which differed from the other families in that table by



FIG. 18. *Oenothera seg. contracta*, in family 40140, six weeks after setting in the experimental field. Photo June 28, 1941.

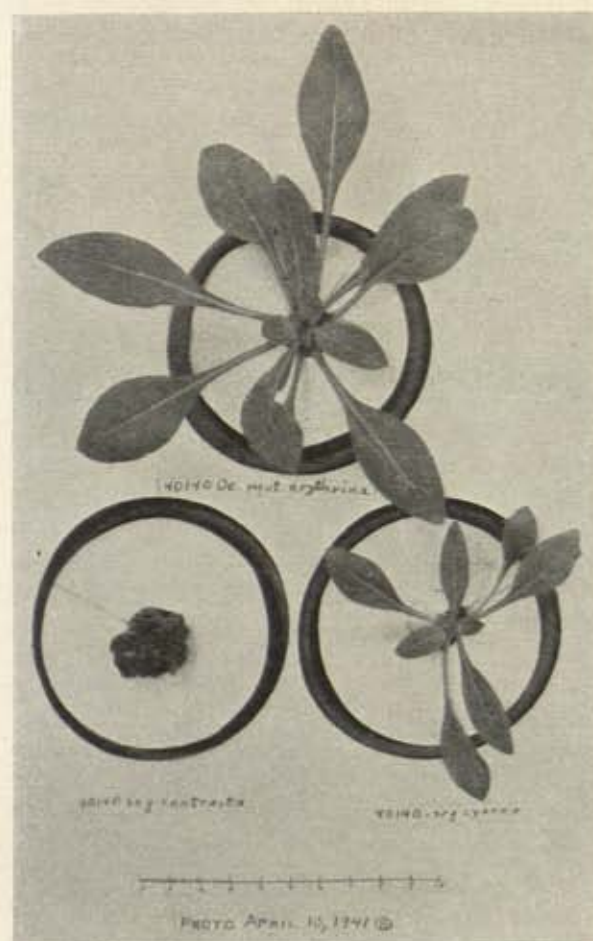


FIG. 17. The three segregates in a family (40140) in which *Oe. seg. cyanea* was added to the expected *Oe. mut. erythrina* and *Oe. seg. contracta*. Photo April 10, 1941.

having, in addition to the two expected phenotypes, *erythrina* and *contracta*, a third unexpected segregating group. In family 39533 such an unexpected group was observed on May 23, 1940, and subsequently given the name seg. *cyanea* because of the notably more bluish-green color. The leaves of this form are considerably narrower, more nearly entire, rather shining and less crinkled than in mut. *erythrina* (Figs. 17 and 19). Like the other segregates from mut. *erythrina*, seg. *cyanea* is of relatively slow growth and has thus far shown no indication of developing a stem in the experimental field, but several rosettes taken into the greenhouse and given long-day treatment were readily brought to sexual maturity, the first flower coming to bloom January 21, 1941. The stem leaves, like the rosette leaves, are narrower and more bluish than the corresponding leaves of *erythrina*. The buds are more slender, but similar as to red pigmentation on the bud-cones. The petals are slightly smaller than in *erythrina*, and tend to be slightly irregular distally with occasionally a lateral lobe reminiscent of *Oe. mut. spathulata* de Vries, one of the trisomic mutants. The petals are almost exactly as wide as they are



FIG. 19. *Oenothera seg. cyanea*, of the family shown in Fig. 17, six weeks after setting in the experimental field. Photo June 28, 1941.

long, 27–30 mm long \times 25–28 mm wide; in other words, they are slightly smaller and relatively narrower than in *erythrina*; (petals of *Oe. mut. erythrina* measure about 34–40 mm long and 45–48 mm wide). The flowers of *seg. cyanea* produced a good supply of pollen, and seeds have been secured both from selfings and from crosses.

Since the *cyanea* segregation adds a third group to a family which was expected to have only the two groups, *erythrina* and *seg. contracta*, it may be assumed that it bears the same genetical relationship to these two groups that *seg. petiolaris* bears to *erythrina* and *seg. decipiens* of the usual strains of *erythrina*. To test this relationship 58 *erythrina* plants in family 39533 were selfed and the resulting progenies grown in 1941 under consecutive family numbers 40135 to 40192, inclusive. Just as *erythrina* sibs of *seg. petiolaris*, when self-fertilized, produce two kinds of progenies, some producing *petiolaris* again while others produce only *erythrina* and *decipiens*, so also it is

found that these *erythrina* sibs of *seg. cyanea* are genetically of two kinds though phenotypically indistinguishable.

These progenies are collected into the two tables, 5 and 6, Table 5 containing all the progenies which included a *cyanea* group and Table 6 all those which consisted of *erythrina* and *seg. contracta* only. The relative numbers of families in these two tables, 36:26, correspond closely with the numbers in the *petiolaris* series presented in Tables 1 and 2, namely, 159 to 109; for $159:109 = 36:24.7$. Much stress must not be laid on this nearly exact duplication of these two ratios, as it may possibly be a mere coincidence, but even if the ratios were less exactly equal the assumption seems to be substantiated that the genetical significance of *seg. petiolaris* in the *decipiens*-bearing families is identical with that of *cyanea* segregates in *contracta*-bearing families. A further test of this conclusion is available, but must await the growing of another generation, when *erythrina* plants from families listed in Table 5 should again give a similar ratio of two kinds of families, while *erythrina* plants from families listed in Table 6



FIG. 20. *Oenothera mut. erythrina*, in family 40140 six weeks after setting in the experimental field. Photo June 28, 1941.

TABLE 5

PROGENIES CONTAINING SEG. *cyanea*, FROM SELF-FERTILIZED MUT. *erythrina* SIBS OF SEG. *cyanea*

Grand-parent Number	Parent Number	<i>Contracta</i>	<i>Erythrina</i>	<i>Cyanea</i>	Other variants or doubtful
38305	39533	25	61	16	4
39531	40131	11	38	6	2
39533	40135	49	47	13	2
	40139	69	71	19	—
	40140	42	68	19	5
	40142	22	28	6	—
	40143	56	59	18	4
	40145	47	61	20	5
	40146	37	45	10	—
	40148	8	23	4	—
	40151	45	67	18	3
	40153	33	44	6	—
	40154	63	72	10	—
	40157	27	61	4	—
	40158	41	56	24	2
	40160	15	50	3	—
	40161	36	85	16	—
	40163	18	39	5	1
	40164	29	53	8	—
	40166	41	54	12	3
	40168	23	50	1	2
	40170	39	44	4	2
	40172	33	44	11	—
	40174	31	45	4	—
	40175	33	45	8	—
	40176	25	62	14	—
	40177	30	49	12	1
	40178	50	68	14	—
	40179	43	75	13	5
	40180	35	70	23	—
	40181	52	83	9	1
	40184	44	31	4	—
	40185	65	88	11	—
	40188	52	77	18	—
	40189	30	47	7	1
	40192	35	56	17	4
Totals (36 families)		1334	2016	407	46

should give no case of segregated *cyanea* in the next generation.

Oenothera seg. diminua, seg. nov.

On May 16, 1939 I found that many of the 207 plants which had been potted in one of my *petiolaris*-bearing families (38516) had died and that there remained 17 plants so diminutive that it was clear that they would not survive to be set into the field. It is probable that nearly all of the 91 plants which had died before this date were of this same depauperate form. I assume therefore

that this family was made up of about 108 seg. *diminua*, 18 seg. *decipiens*, 56 *erythrina*, and 28 seg. *petiolaris*. Two of the *petiolaris* were also

TABLE 6

PROGENIES CONTAINING NO SEG. *cyanea*, FROM SELF-FERTILIZED *erythrina* SIBS OF SEG. *cyanea*

Grandparent Number	Parent Number	<i>Contracta</i>	<i>Erythrina</i>	Other variants or doubtful
39531	40132	23	50	—
	40133	8	31	—
	40134	14	52	2
39533	40137	45	72	—
	40138	93	94	—
	40141	82	85	7
	40144	55	68	5
	40147	12	33	—
	40149	21	43	—
	40150	17	27	—
	40152	47	96	2
	40155	12	24	—
	40156	39	90	—
	40159	66	89	4
	40162	47	68	—
	40165	45	79	2
	40167	14	40	—
	40169	42	86	3
	40171	21	45	—
	40173	30	59	1
	40182	44	87	—
	40183	64	84	2
	40186	20	94	1
	40187	74	95	1
	40190	17	30	1
	40191	32	76	—
Totals (26 families)		984	1697	31

TABLE 7

PROGENIES CONTAINING *Oe. seg. diminua*, FROM SELF-FERTILIZED *erythrina* SIBS OF SEG. *diminua*

Grand-parent Number	Parent Number	<i>Decipiens</i>	<i>Erythrina</i>	<i>Diminua</i>	<i>Petiolaris</i>	Other variants or doubtful
37434	38516	18	56	108	28	1
38516	39498	14	71	49	—	1
	39501	0	74	24	—	—
	40666	3	37	16	—	2
	39502	11	25	14	5	—
	39503	0	26	13	—	—
	39504	3	26	19	10	—
	39505	7	53	47	—	—
	39506	15	64	39	—	3
Totals (9 families)		71	329	432	43	7

TABLE 8

PROGENIES WHICH CONTAINED NO *Oe. seg. diminua*
FROM SELF-FERTILIZED *Oe. mut. erythrina* SIBS
OF *SEG. diminua*

Grandparent Number	Parent Number	<i>Decipiens</i>	<i>Erythrina</i>	<i>Petio-laris</i>	Other variants or doubtful
38516	39496	0	2	—	—
	39497	62	65	33	2
	39499	43	36	26	—
	39500	49	95	—	—
Totals (4 families)		154	198	59	2

diminua, and are duplicated in this formal ratio.

To study this new segregation, eleven *erythrina* plants of family 38516 were self-pollinated and their progenies were grown in 1940 under the consecutive family numbers, 39496 to 39506, inclusive. The results are given in Tables 7 and 8.

Table 7 includes all of the families which again contained *seg. diminua*, together with the original family, 38516, while Table 8 includes the four

families of like origin which contained no *seg. diminua*. Family 39496 had only two plants, both *erythrina*, and may or may not belong in this table. They are included here merely for the sake of completeness of the record. In two families, 39501 and 39503, *seg. diminua* seems to have completely replaced *seg. decipiens*, while in all the other families of Table 7 *seg. decipiens* was present, but in strikingly reduced proportion. The totals for these five families show only 39 *seg. decipiens* to 195 *erythrina* and 135 *seg. diminua*. In 1941 I have repeated family 39501 under the family number 40666. A portion of the seedpan of this family is shown in Fig. 21, where the great contrast in size between *erythrina* and *seg. diminua* can be readily seen. Reference may be made also to Fig. 28, where *Oe. seg. diminua* may be compared with all the other mutational segregates here described except *Oe. seg. sublethalis*. It will be noted that this new test of the parent of 39501 shows again that the *Oe. seg. decipiens* has not been completely replaced, but only greatly reduced in the presence of *seg. diminua*. In two



FIG. 21. Portion of seedpan 40666 showing *Oe. mut. erythrina* and *Oe. seg. diminua* which has practically replaced *Oe. seg. decipiens* in this family.

families, 39502 and 39504, seg. *petiolaris* was also present, and in the former one plant and in the latter two plants seemed to represent the combination, *petiolaris diminua*. When setting family 40666 to the field on May 23, 1941, all of the seg. *diminua* were set to a box of soil in the greenhouse, but by June 12, all had died.

In 1941 I have 12 families from selfed *erythrina* plants in family 39497 and 8 families from *erythrina* plants in family 39499. As both of these parental families contained no seg. *diminua*, these families give an answer to the question

whether seg. *diminua*, like seg. *petiolaris* and seg. *cyanea*, can be transmitted only by *erythrina* plants which are sibs of the particular segregant under discussion. The results from these families, together with 3 similar families grown in 1940, are presented in Table 9 and show that there was not a single specimen of seg. *diminua* among the 1,947 plants included in these 23 families. In other words the ability to produce seg. *diminua* is lost permanently from the *erythrina* component of any family in which these *erythrina* plants had no seg. *diminua* sibs.

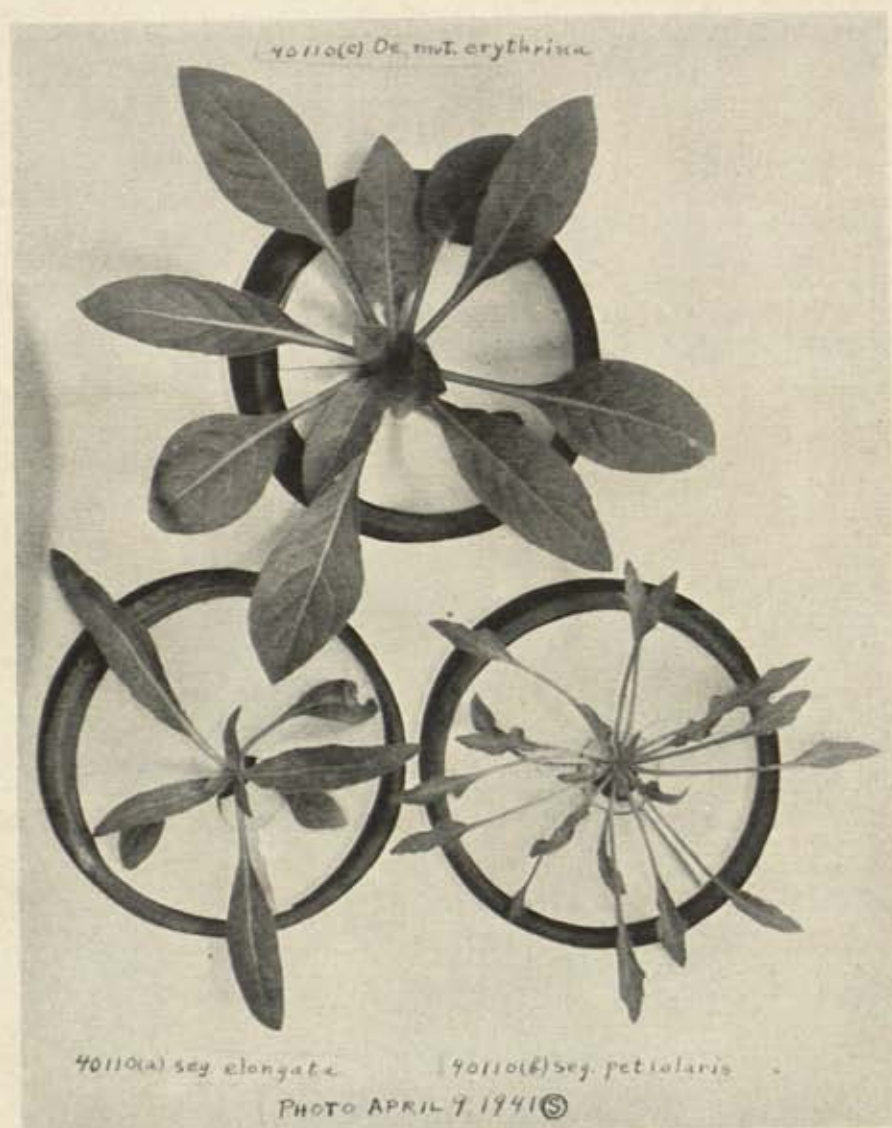


FIG. 22. *Oenothera* seg. *elongata* (lower left) which appeared in family 40110 completely replacing the expected *Oe. seg. decipiens*. The parent type, *Oe. mut. erythrina*, is shown above and *Oe. seg. petiolaris*, which was also present in this family, at lower right. Photo April 9, 1941.

TABLE 9

PROGENIES FROM SELF-FERTILIZED *Oe. mut. erythrina* IN FAMILIES WHICH CONTAINED NO SEG. *diminua*, THAT IS, FROM FAMILIES LISTED IN TABLE 8

Grandparent Number	Parent Number	<i>Decipiens</i>	<i>Erythrina</i>	<i>Petio-laris</i>	Other variants or doubtful
38516	39497	62	61	33	6
	39499	43	36	26	—
	39500	49	95	—	—
39497	40103	31	47	—	—
	40104	32	52	—	—
	40105	36	70	—	—
	40106	13	30	9	—
	40107	32	78	—	—
	40108	16	28	8	—
	40109	50	53	—	—
	40110	—	56	18	10*
	40111	13	27	14	—
	40112	27	43	—	—
	40113	31	41	31	1
	40114	18	37	15	1
39499	40115	22	56	—	—
	40116	30	52	—	1
	40117	41	73	—	—
	40118	12	20	6	—
	40119	34	41	21	2
	40120	17	25	13	—
	40121	28	49	—	—
	40122	5	14	6	—
Totals (22 families)		642	1028	182	11

* These were *Oe. seg. elongata*, as indicated in Table 1. This family is omitted from totals at foot of the table.

Oenothera seg. elongata, seg. nov.

In Table 9 it may be noted that family 40110 was in remarkable contrast with the other 22 families of that table in that it had, in place of the *decipiens* group, an entirely new group which has been named *seg. elongata*, because of the notably longer, narrower leaves. This form was discovered on April 8, 1941, and described on that date as follows: "The first several leaves are *erythrina*-like after which the leaves become stiff, with some lateral veins running almost parallel with mid-rib and margin. Blades often somewhat asymmetrical, the margins somewhat irregularly shallow-repand." A young rosette as of the date when this description was written is shown in Fig. 22 with the other two forms with which it was associated in family 40110. On June 26, 1941, these plants were examined in the field and the rosette leaves of *seg. elongata* were described as "narrow lanceolate, denticulate, often irregularly trough-

shaped." The *seg. elongata* rosettes are shown in Figs. 23 and 28 for comparison with *seg. decipiens* (Figs. 24 and 28) which they have clearly replaced in this family and a typical stem leaf from a point about 30 cm above the rosette is shown for comparison with other relevant forms in Fig. 29. It will be interesting to observe whether the *erythrina* sibs of *seg. elongata* behave consistently in the same manner as the sibs of *seg. contracta*, by producing progenies consisting generally of *erythrina* and *seg. elongata* with *seg. decipiens* nearly or completely omitted. One of the *elongata* plants, 40110 (6), more precocious than the rest, came to bloom in the end of July, and several others have started stems, thus indicating that *seg. elongata* tends to be more precocious than most of the other new forms. This first flowering specimen is shown in Fig. 25. The stem leaves show a continuation of the long lance-like form of the rosette leaves as may be seen by reference to Fig. 29. Buds are more slender than those of *erythrina*, the free tips being more slender and rather closely approximated. The hypanthium of this first specimen to bloom is long and tubular throughout, and none of the other characters

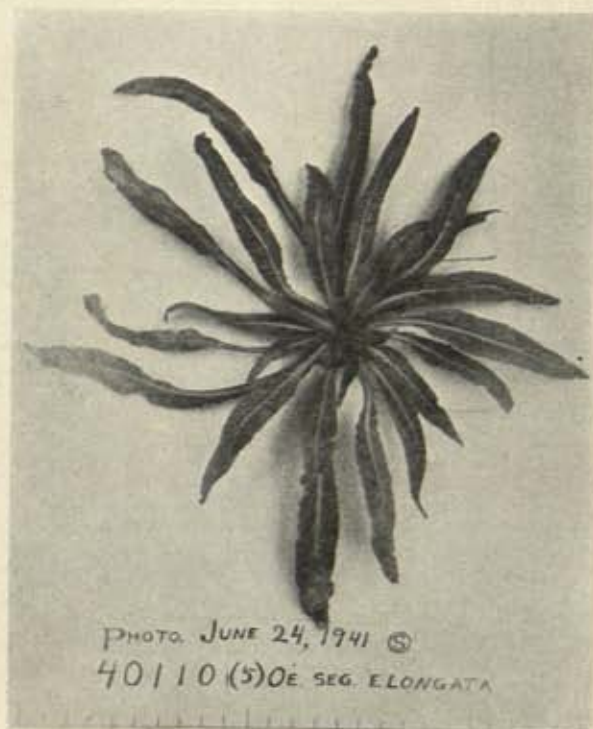


FIG. 23. *Oenothera seg. elongata* (40110) six weeks after setting in the experimental field. Photo June 24, 1941.



suggests any relation to *pollicata*. The flowers are not noticeably different in form and size from those of *Oe. mut. erythrina*. The second plant of seg. *elongata* to reach maturity (40110(5)) differs from the first, by having typical *pollicata* buds and flowers. This inclusion of both *pollicata* and non-*pollicata* plants in the seg. *elongata* group presents an interesting problem for further study. In none of the other new segregants has there appeared such a split with respect to an important characteristic. It seems barely possible that the seg. *elongata* group may be divisible into two groups, an *erythrina elongata* and a *decipiens elongata*, but the evidence for such a distribution is still too meager.

Oenothera seg. retracta, seg. nov.

It will be recalled that family 39531 (see Table 4), among the seg. *contracta* families, contained, in

FIG. 24. Field-grown rosette of *Oe. seg. decipiens* 35245(37) for comparison with seg. *elongata* in Fig. 23. The *decipiens* rosette is three weeks older but at a comparable stage of development. Photo July 18, 1936, by W. H. Brittingham.



• FIG. 25. Habit of the first specimen of *Oe. seg. elongata*, 40110(6), which reached the flowering stage. Photo August 5, 1941.

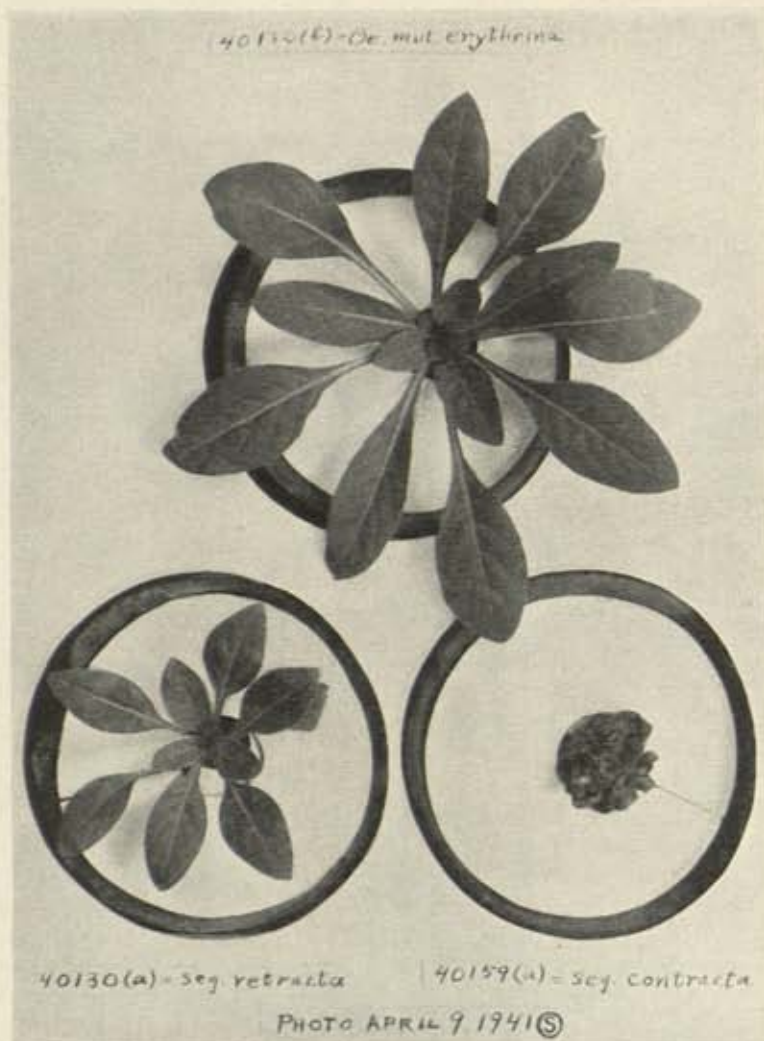


FIG. 26. *Oenothera* mut. *erythrina* and *Oe.* seg. *retracta* (lower left), the two types found in family 40130, where only *erythrina* and seg. *contracta* were expected. *Oe.* seg. *contracta* of same age from another family (40159) is included for comparison with seg. *retracta*. Photo April 9, 1941.

addition to *contracta* and *erythrina*, a new group whose identity remained in doubt. To get further information regarding the segregations in this family five of the *erythrina* plants were self-pollinated, and the resulting progenies were grown this year under the consecutive numbers 40130 to 40134, inclusive. Three of these families have consisted jointly of 45 *contracta*, 134 *erythrina* and 2 slightly aberrant plants of unknown identity. Family 40131 consisted of 11 seg. *contracta*, 6 seg. *cyanea*, 37 *erythrina* and 2 slightly aberrant.

But most notable was family 40130 in which a new uncrinkled segregate similar to mut. *erythrina*

but smaller and darker green completely replaced seg. *contracta* (Fig. 26). These were observed on April 8, 1941, and have been recorded as seg. *retracta*. There were 9 of these to 32 *erythrina*. Four of the smaller *erythrina* plants were at first grouped with the seg. *retracta*, but after setting these to the field, they soon became typical *erythrina* plants, while all of the seg. *retracta* plants died. This remarkable replacement of seg. *contracta* by seg. *retracta* may be considered a partially reversionary change, in view of the fact that the extremely crinkled seg. *contracta* had replaced in similar manner the very slightly crinkled seg.

decipiens. A full test of the *erythrina* plants in this family is contemplated for next year. I anticipate that they will be found to segregate regularly *seg. retracta* and *erythrina*. The failure of *seg. retracta* to withstand setting to the field demonstrated that it is a much weaker form than the original *seg. decipiens*, which it now seems to represent in this particular progeny of *erythrina*. The *erythrina* plants of this family are indistinguishable, however, from those in families which yield normal *seg. decipiens* and from those that yield *seg. contracta*, or any of the other new mutational segregates.

Oenothera seg. sublethalis, seg. nov.

For several years I have had a strain of mut. *erythrina* which has been characterized by the low frequency of occurrence of *seg. decipiens*, and which I have recorded as "non-splitting *erythrina*." The beginning of this strain was made by self-fertilizing an *erythrina* specimen, 35239(98), in one of my *petiolaris*-bearing families in the summer of 1936. The family is recorded in the beginning of Table 1, and the progeny produced by selfing 35239(98) is recorded in Table 2, under the family number 36304. Family 36299 in Table 1 represents the same or a similar strain of "non-splitting *erythrina*," produced by self-fertilizing individual number (90) in family 35239. These two families, 36299 and 36304, had jointly 2 *seg. decipiens* to 174 *erythrina*, the former having in addition 29 *seg. petiolaris*, the latter having no *petiolaris*. All the families descended from these are given in the first half of Table 10, together with these two initial families.

A similar or identical mutational segregation seems to have occurred in an *erythrina* individual 38300(89), for this individual, self-fertilized, produced the descendants entered in the last section of Table 10. In three of these families, 40126, 40127, 40129, there was seen a total of 9 very tiny stiff rosettes practically devoid of chlorophyll, and the same form may have occurred in family 40128, as four plants had died in that family before it was studied on April 4, 1941, only two weeks after the plants had been set from the seedpan to 75 mm pots. This form is denominated *seg. sublethalis* and is seen to offer a rational explanation of "non-splitting *erythrina*," for it seems reasonable to suppose that just as *seg. contracta* and *seg. elongata* have replaced *seg. decipiens* in their respective families, *seg. sublethalis* may have

TABLE 10
PROGENIES FROM SELF-FERTILIZED "NON-SPLITTING"
Oe. mut. erythrina

Grandparent Number	Parent Number	<i>Decipiens</i>	<i>Erythrina</i>	Other variants or doubtful
35239	36299	0	89	29*
	36304	2	85	—
36304	37411	1	20	—
	37412	1	20	—
37411	38293	0	56	1
38293	39486	3	35	—
	39487	1	42	—
38300	39530	1	86	3
39530	40126	0	33	4†
	40127	0	8	3†
	40128	0	31	1
	40129	0	9	2†
Totals (12 families)		9	514	

* These were *Oe. seg. petiolaris* which were not out of place in this family, since the parent *Oe. mut. erythrina* was a sib of *petiolaris*.

† These 9 plants were *Oe. seg. sublethalis*.

replaced *seg. decipiens* in the three families listed in Table 10.

The few plants of *seg. sublethalis* that have been found have disappeared almost immediately after they were observed, and unless special attention were given to finding them in the seedpan, they could be overlooked very easily, and may have disappeared before the plants were potted. Quite possibly also the *seg. sublethalis* genotype is so ineffective that most of the seeds do not even germinate. The production of a nearly true-breeding *erythrina* in this putative way would make the *erythrina* of this particular strain agree closely with the balanced lethal situation seen in *Oe. Lamarckiana*. The percentage germination in most of these families has been disappointingly low, but this cannot be attributed solely to the elimination of a putative *sublethalis* segregate. This strain merits a more thorough study.

DISCUSSION AND CONCLUSIONS

In reviewing this remarkable series of new mutational segregations from *Oenothera mut. erythrina*, it appears that we are dealing with two unique genetical phenomena, (a) the replacement of a previously recurring segregated class of indi-

viduals by a new recurrent class of segregates so unlike the replaced class that it is illogical to think of the new class as merely a modification of the old class, and (b) the addition of a whole new class of repeatable segregates to the previously known and expected classes.

One fact which has greatly facilitated this study and added to the definiteness of the results, has been that most of the new types are so strikingly unlike both *erythrina* and *decipiens* that there have been almost no errors of classification. Such errors have been common in attempts to separate mut. *erythrina* and seg. *decipiens* in the past, but such strikingly unique forms as seg. *petiolaris*, seg. *contracta* and seg. *elongata* can never leave a doubt as to the accuracy of their classification. Among the new forms there have been some errors

in separating seg. *retracta* from *erythrina*, and some error might conceivably occur at an early stage of development in separating seg. *cyanea* from mut. *erythrina*. In regard to such errors as have been made in separating these new forms from mut. *erythrina*, it may be pointed out that these were made in the first families in which the given mutational segregates were discovered. More experience may enable an observer to make a more clean-cut separation of these new forms from the type of their parent.

Whatever the exact mechanism which is operating here, we are justified, because of the relative rarity and the relative permanence of the changes, in recognizing the occurrence of such remarkable replacements and additions of whole classes of recurrent segregates, as of mutational nature.

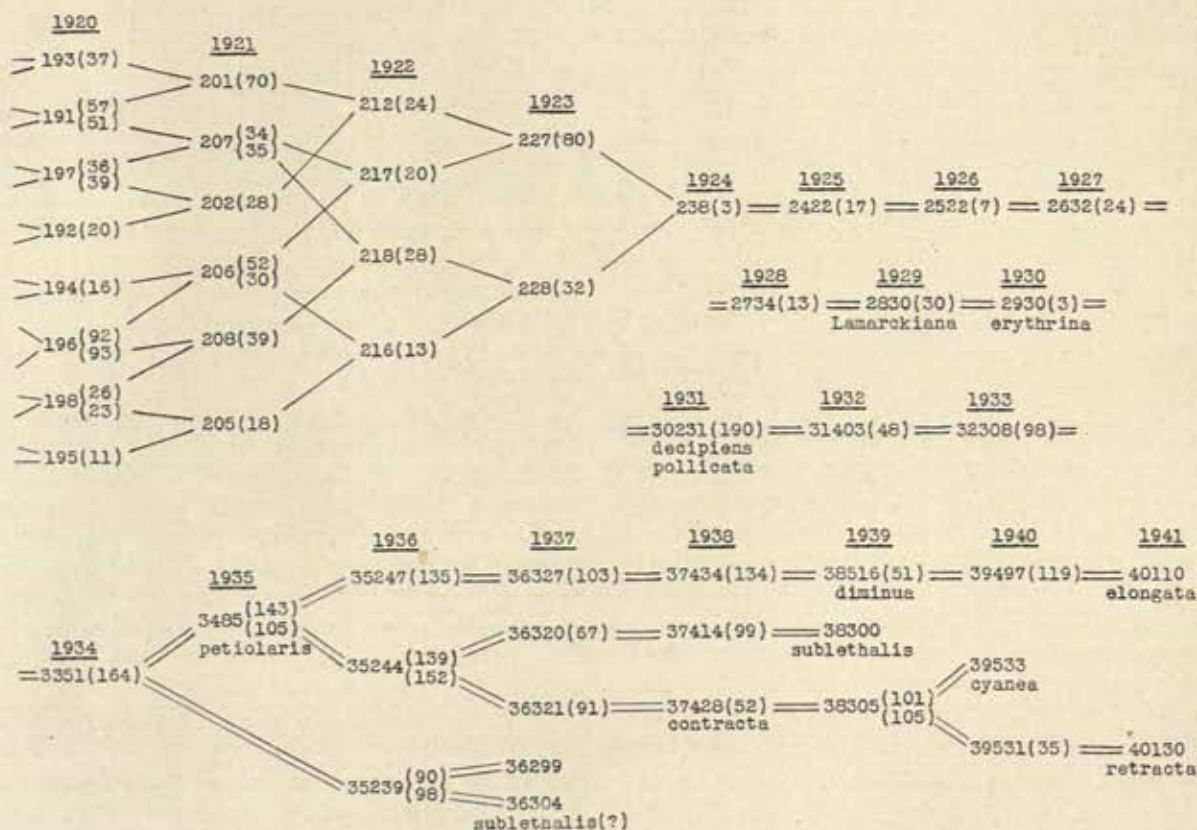


FIG. 27. Pedigree chart for all of the new mutational segregates described in this paper. Double lines indicate self-fertilization. Each number in parenthesis represents a single individual in the family to whose family number it is appended. To the left could be added fourteen additional generations of controlled cross-breeding in the manner indicated by the first generation given in this chart. Previous to 1905, breeding was uncontrolled in a state of nature. All individuals represented on this chart up to and including 2830(30) and all in the fourteen preceding generations of hand-controlled pollination not here included were typical *Oe. Lamarckiana*, and every individual in the chart, including and subsequent to 2930(3), was a typical *Oe. mut. erythrina*. The names of the several new mutational segregates are inserted beneath the pedigree numbers of the families in which they severally made their first appearance. The individuals indicated by the numbers in parenthesis appended to these family numbers were *erythrina* sibs of the indicated mutational segregates.

A study of the pedigree records has brought to light the interesting fact that all of these unexpected new segregates have arisen in a single strain of *erythrina*. The pedigree, complete from 1920 to 1941, is shown in Fig. 27. The double lines in this pedigree chart indicate that the parent represented by the preceding pedigree number was self-pollinated. The progenies included in the tables, all of which are descended from individuals whose pedigree numbers appear in the pedigree chart, represent the offspring of a total of 400 selfed *erythrina* plants, and of these not more than 12 produced obvious mutational segregations. This indicates that the frequency of such mutations in this material is of the same general order as that of the more common types of individual mutations, whether chromosomal mutations or gene mutations.

The fact that these mutations have all occurred in a single strain of *erythrina* is not an accident, but is conditioned by the fact that only in this strain has there been such an extensive program of progeny-testing. The question is an intriguing one, whether a similarly extensive series of tests would bring to light a similar frequency of mutational segregations in other *erythrina* lines unconnected with the one involved in the present paper. It is not likely, of course, that any of these same mutated forms would be duplicated in material of another origin, for none of them has been duplicated in my cultures except perhaps in the case of seg. *sublethalis*, which seemed to originate in two different individuals of the same family, and also in another family several generations removed from this. One might suppose that even in this case there is no identity of the three mutations, since the elimination of a class by the presence of a lethal can hardly be assumed to prove the identity of the death-dealing agency in the three cases. Only when it is possible by genetical or cytological analysis to demonstrate that two lethals occupy identical loci is there ground for the assumption that they represent a repeated mutation.

Too little is yet known regarding the mechanism of inheritance in the *Oenotheras* to allow us even to speak of loci in the ordinary sense except perhaps in the case of the linkages among genes in what I have called the 3rd linkage group, and which are believed to be associated with the paired 1·2/1·2 chromosomes.

There is little basis for a discussion of a putative relationship of the mutational segregations here recorded and the occurrence of segmental inter-

changes, but it may be conceived that a segmental interchange which should result in associating a *decipiens*-bearing segment in the circle with the chromosome which carries the lethal factor and releasing from such association some other segment characterized by a previously hidden recessive, such as seg. *contracta* or seg. *elongata*, would result in a replacement of seg. *decipiens* by the new segregated group. The "additional" types such as seg. *petiolaris*, seg. *cyanea* and seg. *diminua* present still more difficult problems, but might be assumed to involve an interchange between two chromosomes other than that which carries the *decipiens* genes, thus leaving the relations between seg. *decipiens* and mut. *erythrina* unchanged.

Cleland (1929) has reported that the occurrence of double non-disjunction is a rather frequent type of irregularity in the zigzag arrangement of the chromosomes of *Oe. Lamarckiana*, and the same may well be the case in *Oe. mut. erythrina* as well. While this might seem a fairly simple method of transferring a chromosome from one Renner complex or genome to the other, and compensating by removing another chromosome from the second genome to the first, there is a prime obstacle in the way of using this occurrence as a mechanism to explain the peculiar replacement of a well-known type of segregate by a wholly different new type, as recounted in this paper. There is incontestible evidence for the view that every one of the known 14 chromosome-ends is of vital necessity for the existence of a successful individual in the genus *Oenothera*, but no double non-disjunction is conceivable which would not result in the omission of one or more of these indispensable ends. It seems much more likely that the phenomena presented in this paper represent the genetical consequences of a corresponding number of segmental interchanges, by which portions of chromosomes have been transferred from one genome to another without the omission of any vitally necessary part of the genotype.

Cleland (1942) has recently shown that there are 24 different ways in which mut. *erythrina* can be produced from *Oe. Lamarckiana* by the coincidence of only two segmental interchanges. These possibilities should provide for a considerable number of genetically different biotypes of *erythrina*, but not for the full number of 24 different kinds, since in those cases in which both of the putative interchanges have occurred within the same Renner complex, *velans* or *gaudens*, the gene

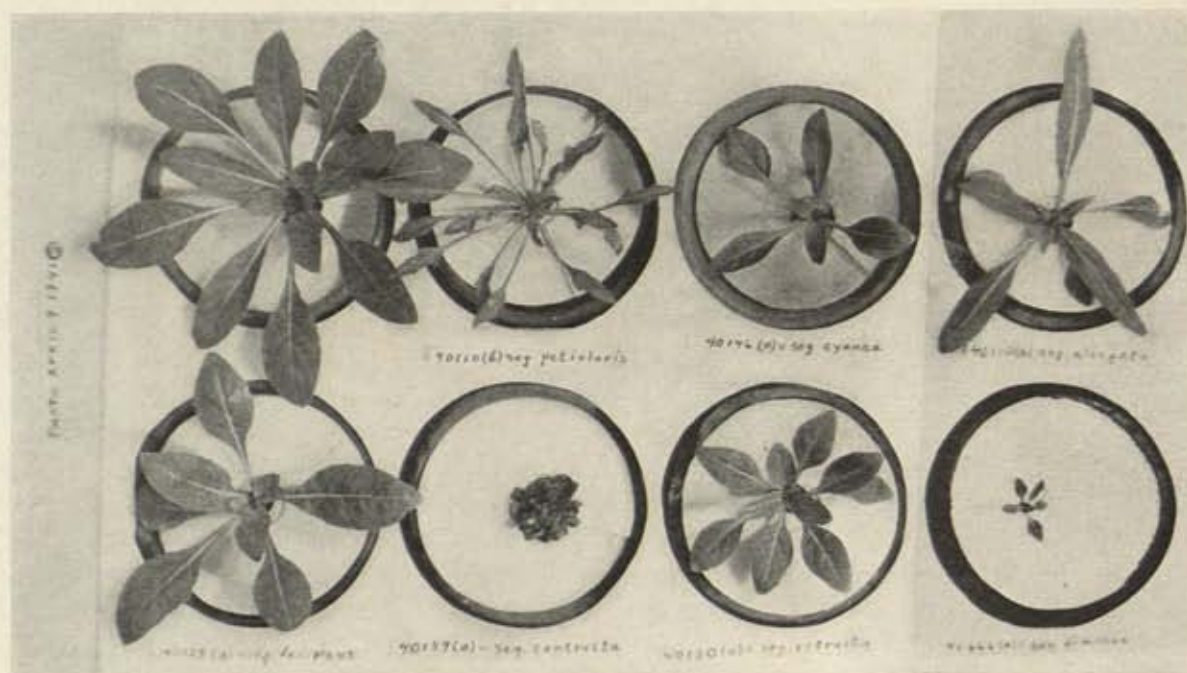


FIG. 28. Recapitulatory photograph of *Oe. mut. erythrina, seg. decipiens*, and all of the new mutational segregates here described except *seg. sublethalis*. Of the latter the entire rosette could be covered by a single leaf of *seg. diminua*. Photo April 9, 1941.

content of the *erythrina* so produced would remain unchanged. These putatively different biotypes of *Oe. mut. erythrina* can have no significance, however, for the genetical phenomena recorded in this paper, for although there are these 24 ways in which *erythrina* might originate from *Oe. Lamarckiana*, the material involved in this paper can have possessed originally only one of these; all are descended by controlled self-fertilizations, from a single original *erythrina* mutant 2930(3), in a line of *Oe. Lamarckiana* which also had been selfed for six years before this *mut. erythrina* appeared (see pedigree chart, Fig. 27).

The new forms produced by mutational segregation in this material offer but limited opportunity for the student of segmental interchange because of the difficulty in getting them to develop to sexual maturity or to be usable for breeding. Thus far, *seg. petiolaris*, *seg. cyanea*, *seg. elongata* and *seg. contracta* have been induced to flower and fruit, but only in small numbers and with considerable difficulty. *Seg. petiolaris* has been found by Catcheside to have a circle of 6 and 4 pairs of chromosomes. Probably *seg. cyanea* will be found to have the same configuration, but whether those forms which are replacing *seg. decipiens* have, like it, an absence of catenation can-

not be determined if they do not bloom. A cytological investigation of meiosis in F_1 hybrids between the different individuals of *erythrina* which have unlike segregational derivatives might prove illuminating.

SUMMARY

Oenothera mut. erythrina, a well known half-mutant, normally produces a progeny consisting of two types of plants, one of which repeats the parental genotype, *erythrina*, the other a true-breeding type known as *seg. decipiens*. This paper reports the occurrence of seven new mutational segregations from *erythrina*, which are described under the names *petiolaris*, *contracta*, *cyanea*, *diminua*, *elongata*, *retracta*, and *sublethalis*. Several others have been observed but not yet adequately studied.

Of these, *seg. contracta*, *seg. elongata*, *seg. sublethalis* and in some cases *seg. diminua* have replaced *seg. decipiens* and *seg. retracta* has replaced *seg. contracta*.

Seg. petiolaris has been added to families which had the normal proportions of *erythrina* and *seg. decipiens*, and in like manner *seg. cyanea* has been added to families which had the otherwise normal ratios of *erythrina* and *seg. contracta*.

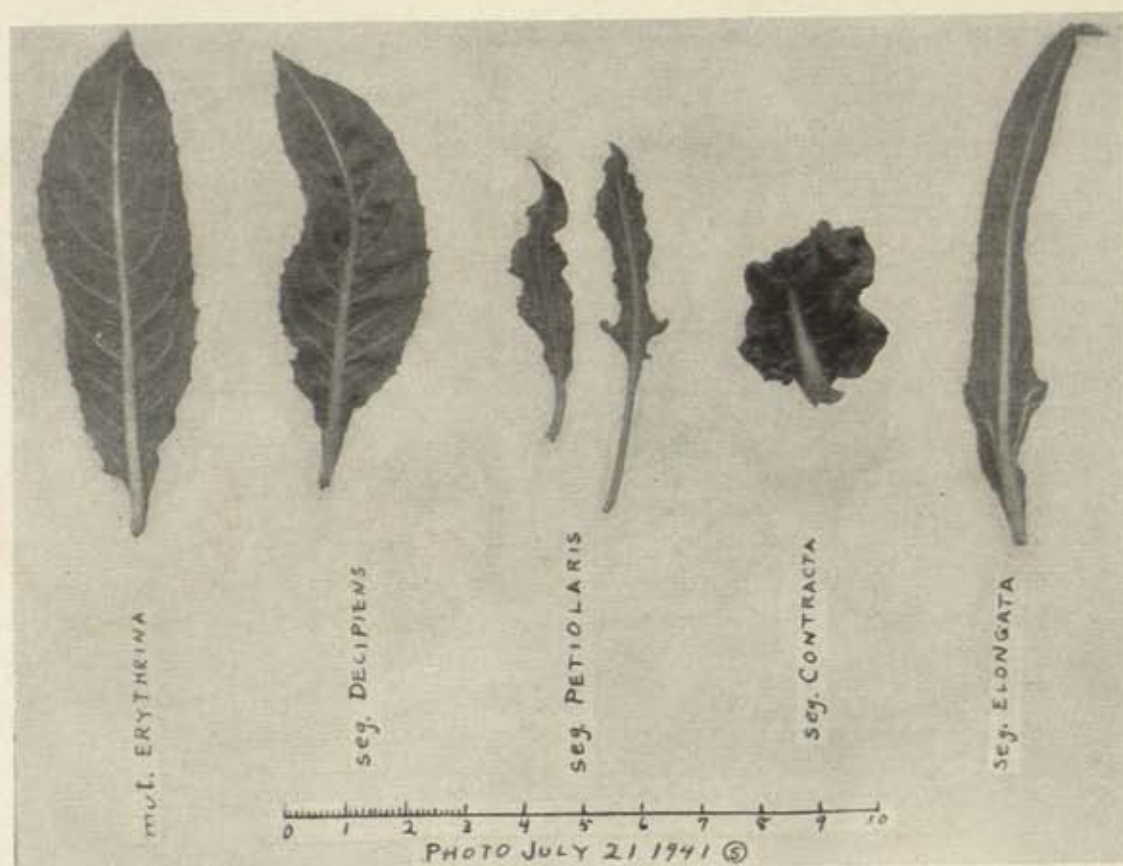


FIG. 29. Stem leaves taken from the central axis about 30 cm above the rosette, for comparison of *Oe. mut. erythrina* and four of its mutational segregates, *decipiens*, *petiolaris*, *contracta* and *elongata*.

About three-fifths of the *erythrina* plants in a family which contains *petiolaris* will yield *seg. petiolaris* offspring. The rest give progenies containing mainly *erythrina* and *seg. decipiens*, no *petiolaris*.

In like manner about three-fifths of the *erythrina* plants in families containing *seg. cyanea* produce *seg. cyanea* in turn in their offspring, while the remaining two-fifths produce only *erythrina* and *seg. contracta*.

Erythrina plants in families which do not contain *seg. petiolaris*, *seg. cyanea*, or *seg. diminua*, respectively, seem to have lost the power to produce these forms in their progenies.

The replacement of *seg. decipiens* by *seg. sublethalis* has brought about approximately the balanced-lethal condition long recognized in *Oe. Lamarckiana*, thus giving a nearly true-breeding strain of *erythrina*.

All of these new mutational segregations result in plants of inferior physiological vigor, or at least of slower development, but *petiolaris* and

elongata have come to bloom, in a relatively few cases, naturally in the experimental field but only late in the season. *Seg. petiolaris* and *seg. cyanea* have been successfully brought to maturity in the greenhouse by the application of long-day treatment.

Seg. contracta was not induced to flower by means of long-day treatment, but several specimens have produced stems after a summer and winter of partial protection in a coldframe, and have finally produced several flowers.

The difficulty in securing flowers puts obstacles in the way of studies of catenation in these forms but the chromosome arrangement in *seg. petiolaris* has been determined for me by Dr. D. G. Catcheside. The arrangement is the same in this segregate as in *erythrina*—a circle of six and four pairs.

It is tentatively assumed that the replacements of the usual *seg. decipiens* and additions of other new mutational segregations result from segmental interchanges which change the association of the

segments involved with respect to a segment containing the putative lethal factor.

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MONTAGNAIS-NASKAPI BANDS AND FAMILY HUNTING DISTRICTS OF THE CENTRAL AND SOUTHEASTERN LABRADOR PENINSULA

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CONTENTS

Introduction.....	215
History, Population, and Faunal Correlations.....	217
Local Bands.....	218
Moisie and Petisikapau.....	224
Ste. Marguerite and Kaniapiskau.....	227
Shelter Bay.....	232
Nichikun.....	232
Michikamau.....	234
Conclusion.....	238

ABSTRACT

Ethnological material dealing with the hunting territory concepts of the Montagnais-Naskapi Indian bands of the central and southeastern Labrador Peninsula is presented and analyzed in the light of present knowledge of the ecological relationships existing between these people and their faunal and floristic background. The frontier dividing the tundra from the forest is regarded as the factor determining to a considerable extent the practice of communal as opposed to dispersed hunting with its attendant patterns of family ownership of hunting territories. It is further observed that among some groups the two types of hunting system may both be practiced but under different environmental pressures. A sequence of phases in the development of the institution of the family hunting territory is tentatively proposed.

In a past number of the *American Anthropologist* Speck presented material gathered in the field and compiled, with reports of earlier writers, the material obtained by him through a number of years' investigation of the constituency and territorial locations of some twenty-six local bands of the Montagnais-Naskapi Indians of the Labrador peninsula.¹ In the same article the attempt was made to give some of the social characteristics pertaining to these band subdivisions and to discuss economic features which seemed to influence the social pattern. The material used in the preparation of the article in question included some material that was still unpublished relating to certain bands in the

eastern and southeastern regions of the peninsula. The purpose of the present report is, then, to bring out the data concerning the formation of those bands just referred to, giving the details from notes, made from 1922 to 1925, while work was proceeding in the lower St. Lawrence area. In the general article referred to above, reference was made to a series of reports previously published, which presented similar outlines of the bands in other parts of the peninsula. The present material covering the characteristics of the Ste. Marguerite, the Moisie, the Shelter Bay, the Michikamau, the Nichikun, and several other now almost disintegrated groups concludes the collection of material now on hand regarding the boundaries and family composition of the native divisions for this immense region.

The purpose in bringing out the material is to make available the long-shelved notes on the bands investigated over fifteen years ago as a contribution to our knowledge of the social framework of Algonkian peoples of the higher latitudes. Half a generation has elapsed since these data were recorded and inevitable changes have occurred in the bands.

A curious circumstance of the field work which produced the material offered in the study lay in the fact that the investigation of geographical ethnography was carried on before the region under consideration had been mapped. It was accordingly upon the geographical knowledge retained in the memory of the Indians and their ability to demonstrate it on the inadequate charts only available at the time, that the demarcations of hunting grounds were based. Several examples of the cartographic faculties of the hunters as made with pencil were obtained. They are reproduced in Figs. 1 and 2. For the limited areas which they cover they show details of surface of land and water the like of which will

¹ Vol. 33, No. 4, October-December, 1931, pp. 557-600.

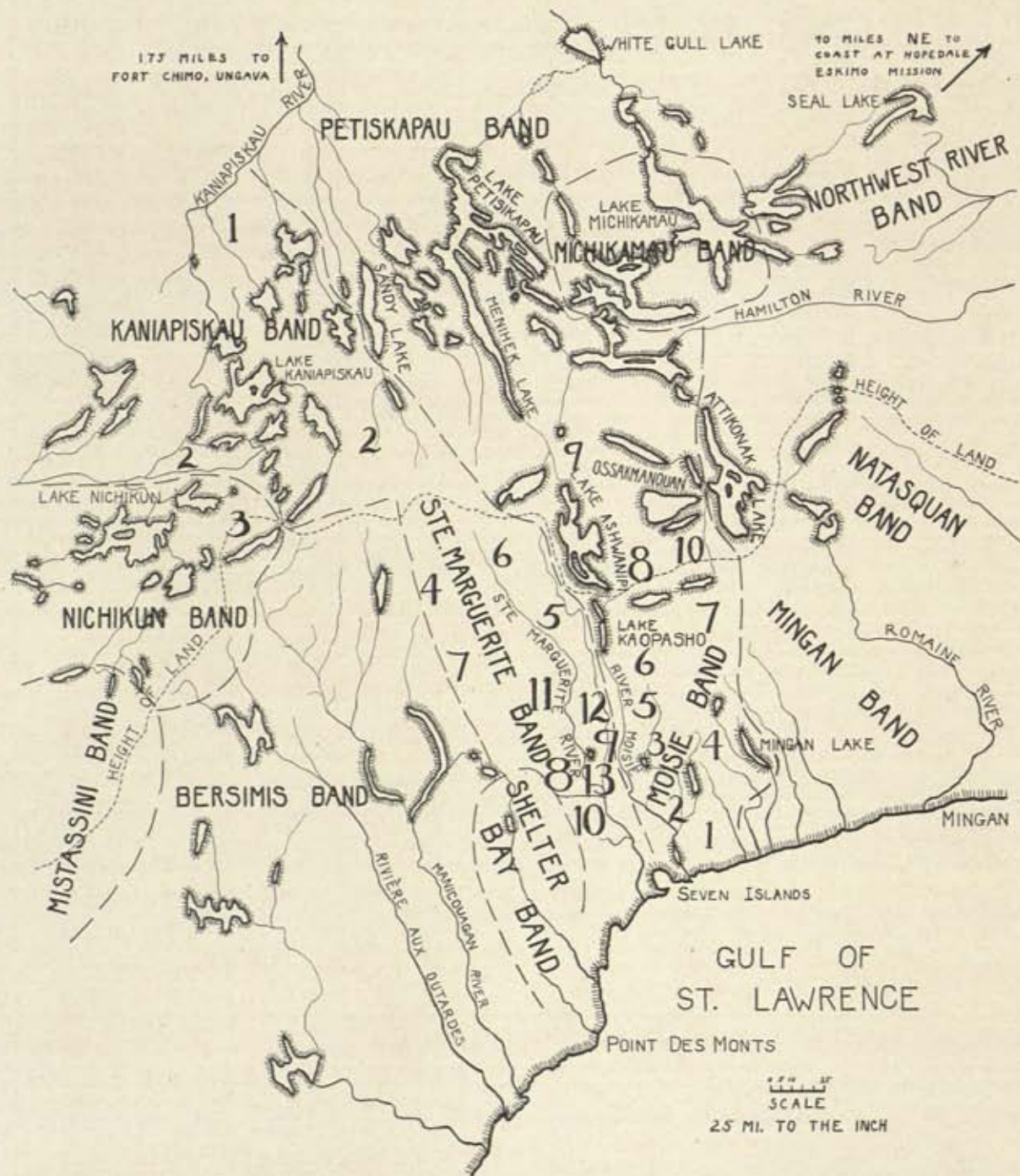


Chart showing distribution of Montagnais-Naskapi Bands of the Lower St. Lawrence and Labrador Peninsula, with approximate location (in numbers) of Family Hunting and Trapping Districts (1922-25). (Drawn by F. Staniford Speck.)

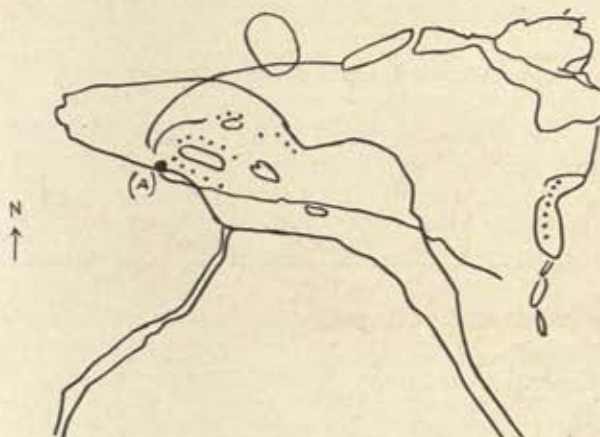


FIG. 1. Sketch map of Pien Andre's winter camp on *Kamacko'gan cakhi'gan* (lake) at head of branch of Ashwanipi River (near Petisikapau Lake) during mid-season separation period (1924-5). Drawn by himself.

Explanation.—At A, Andre's two-fire wigwam of caribou skin, his headquarters. The dots around the islands and along shore denote sets of fish-hooks under ice; 4 below the nearest island, 6 on north side of same island, 8 on far side of other island and along shore.

Division of Labor.—One man takes care of each set of hooks, three in all. Two men take road to mountains on northeast of big lake and go to lake system (upper right) for caribou. When wind blows too hard on this circuit to permit returning by same way over mountains, they turn southward to lake marked by fishing sets (dots on lake at lower right) and strike overland and across ice on big lake directly to headquarters camp A.

The continuous lines represent the routes taken by the men who tend the fishing and the trails of the hunters on land and ice.

not be indicated on printed maps for a long while to come.

In this cartographic interest the Montagnais-Naskapi seem to vie with the Eskimo. Their ability to represent the lake and river features of their own hunting districts as well as of more distant waterways and portages is a definite acquisition of their culture. Explorers of the Labradorian plateau have noted the accuracy of travel charts drawn upon sheets of birch-bark with charred wood from the days of Napoleon Comeau and A. P. Low, down to the observations of Belanger and others, who availed themselves of the plottings to find a way in hitherto uncharted areas. The cartographic faculty has another bearing here upon our quest for details of the background of native land knowledge. It brings out the fact that geographic nomenclature is also a well-developed element of the hunting existence from one end of the sub-arctic forest civilization to the other. In recording the loca-

tions and tracts of hunting and trapping among the bands treated here, the names of most bodies of water were given by the men as known to them in their peregrinations. Some of the names entered are to be found in French or English orthography on the published charts available. Others, however, are apparently the names of lakes known only to the native habitués of the more remote regions. These have caused some vagueness in the delineation of band as well as family *endroits*. Undoubtedly corrections will later be made in the boundary indications given on the map accompanying the report when a more detailed geographical check-up shall have been made. The name listings in the present report will, however, serve as an indication of the familiarity possessed by the men, not only with the terrain itself but also with the unwritten literary nomenclature of their extensive ranges.

Reverting for a moment to the general field of inquiry, we may point out that in the social-economic systems of practically all the Algonkian-speaking peoples so far investigated (inhabiting the area between latitudes forty-five degrees and fifty-two degrees, between the Atlantic and Lake Winnipeg chiefly north of the Great Lakes and within the drainage of the lower St. Lawrence), the recently much-discussed institution of pre-

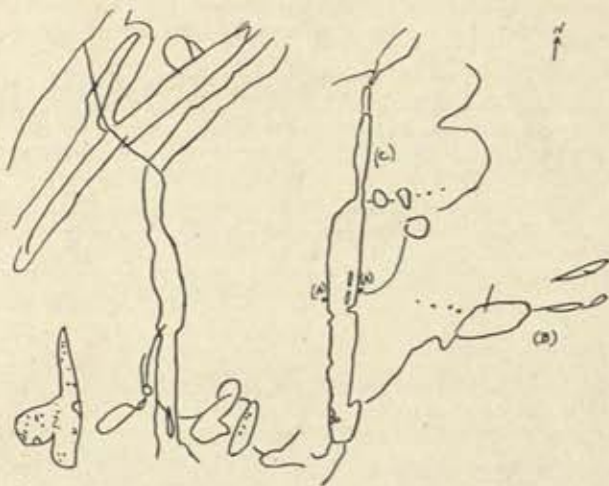


FIG. 2. Sketch map of districts hunted and trapped by Alexander Mackenzie's party, between Menihék and Petisikapau lakes, and on Petisikapau River during winter operations (1924-5). Drawn by himself. Lower left *Katsagwunakajo* lake (dots denote islands), left center Petisikapau River, right center *Ketcemateo pitcuau* Lake.

Explanation.—A, Alexander Mackenzie's headquarters camp, two divisions. B, at right and upper right center, location of marten trapping areas. Dots on land areas denote winter trails.

empted paternally inherited family hunting territories has been observed. It does not occur in a single case in eastern North America among other than Algonkian tribes except where alien native culture has been in contact with them and may be suspected accordingly to have been modified in this direction by them. An instance of this is to be noted among the Iroquois who consistently fail to show possession of the trait except in the case of the Iroquois of Oka, P. Q., where it has been introduced through territorial adjacency and social association, even cohabitation, with Algonkian peoples.² At the same

² Horace T. Martin in his work on the Canadian beaver entitled *Castorologia* (Montreal 1892) makes a tantalizing reference to a portion of the old beaver hunting territory of the Six Nations lying between Lake Champlain and the St. Lawrence. He speaks as follows (p. 140): "In some cases in the interior of our country, near the height of land, these hunting grounds are still recognized as the rightful property of certain Indian families, and curiously, the line of descent is on the mother's side, so that travellers relate how many an old decrepit squaw is honored and propitiated for favors from her beaver reserve. These reserves were held with as much exclusiveness as a freehold estate in England, and to trespass or to poach on them meant to jeopardize one's life. The question of ownership involved all the mystic relations of the social career of the Indian geneologies, tribal affinities, questions of taste and preference, but also rested greatly in the first instance on the right of might. . . ."

This area, at the time of the French and Indian wars was, from a cultural standpoint, mixed Iroquois and Algonkian. It was really St. Francis Abenaki country—and the St. Francis Abenaki were largely influenced in culture during the historic period by the Mohawk. We have no direct evidence, however, that they adopted a maternal clan system, which would, of course, have placed mother right ahead of father right in respect to land.

Martin, who was not an ethnologist, may have been led into making the statement quoted above through a perfectly natural mistake. Among the northern Algonkian widows were title-holders to hunting land and so were often sought as wives by men who thereby got a hunting estate. Widows advanced in age are often married by young men for such a reason. This superficial observation could easily lead to interpretations involving matrilineal descent of the territories. It must be reiterated that we know of no other instance of *regular* descent on the mother's side though women may have potential claims upon a father's hunting territory should they have to resort to it to avoid famine in case a husband's tract should fail to yield sustenance for a year or so.

The senior writer's observations at Seven Islands are perhaps typical of the variation in practice which is observable even among the Algonkian. Speck found it possible to induce several of the hunters to discuss what they regard as a normal method of procedure in transmitting the use of their territories from one generation to the next. In recording the data on family history and control of the districts in family succession among the

time we find that the hunting institutions of the Algonkian north of the fifty-second latitude undergo a change from the aspect of affairs that we encounter in the heavily forested region nearer to the St. Lawrence and the Great Lakes. In the latter area the local bands are found subdivided into small family groupings that hunt by themselves throughout the winter, while in the former zone the family groups remain together forming the "large family" bands with more communal hunting customs than those just south of them.

The bands to be treated in this article include both types, and therefore some discussion will be included as to the meaning and possible history of this modification in social pattern of two purely hunting types of society whose other institutions and history seem to be practically identical in derivation. Before indulging in extended speculation as to what causes may have induced the separation of the types and what circumstances may have encouraged their development along one line or another, the substance of information on the make-up of the central and southeastern bands may be considered.

As our understanding of theoretical circumstances involved in the formation and subsequent trend of growth of these bands gets better, so too the collections of pertinent data will improve, and we shall acquire study material out of which should emerge some conceptions of their history superior to those now achievable. Dr. Hallowell's recent ideas, after consideration of cross-cousin marriage practices, actual and implied in the north, and the taking of geneologies, with his testing of matrilineal tendencies in the cohesion of families, exemplifies the kind of progress being made in our approach to an under-

bands who make rendezvous at Seven Islands, a generalized statement was made which represents the sum-up of custom among these hunters. It seems that a hunter who works a certain tract of territory will say that he continues to occupy it by right derived from his father in most cases. Some of them reside with and work trapping and hunting grounds with the wife's father—patrilocal association. This affiliation arises when a hunter has no sons to receive the legacy of usufruct from his line. "His daughter brings her husband to join the father-in-law's family," was the customary response. Women and children thus had an option in living with either the father's or mother's family, according to the social opportunities offered by each, plus the need for their labor coöperation, and especially determined by the prospects of abundance of the food and fur resources of the lands on one or the other side of the family.

standing of the forces at work in moulding social structure among the northern Algonkian.³

Our conclusions will show the established truth of the assumption suggested in several previous articles that there are two types of social development at work among the northern Algonkian, associated evidently with their occupation of one or the other geographical zone types, the taiga or the tundra of the Labrador peninsula and the lower St. Lawrence and Hudson Bay area. Of the two types one is nomadic and communal in structure as regards the grouping of biological family units to form a collective band. It occupies the open tundra north of the forest zone where the Barren Ground caribou is an economic mainstay. The second type is based upon the more sedentary limited nomadic family principle and seems to remain confined to the coniferous forest area. The factor operating chiefly to determine the two is, we believe, traceable in large degree to the natural history of the game animals which alone furnish the natives of the Labradorean area with their subsistence. The governing factors may be recognized as lying within the influence of the seasonal changes affecting the movements of flesh-yielding and fur-bearing animals with its attendant stress and famine circumstances. Both types prevail in the social program of the same band at different seasons, that is, the collective family horde breaks up into the small-family group hunting as a biological unit within a limited often paternally inherited district, or vice versa. This is known as an actual fact from direct contemporary information and from printed statements of French and English authors who first encountered these famine-bred cultures of the subarctic.⁴ The point deserves more weight in our study of the subject as investigation proceeds. Caron is one whose remarks are clear-cut and

definitive enough to merit reference.⁵ Alluding to the bands on the upper St. Maurice (the Têtes de Boule) he observes: "Mais la famine augmentant sans cesse, il fallut en venir à se séparer, en effet, par petites troupes les sauvages avaient pliés la chasse de résister à la famine, et si une troupe mourait de faim, et de misère, on pourrait espérer que les autres seraient épargnées." ("But famine increasing without check it became necessary for them to separate. Accordingly, in small companies the Indians pursued the chase to avoid starvation, and should one company die of famine or of misfortune, it could be hoped that the others would be spared.")

Reference to the two modes of hunting just discussed is manifest in the remarks of Davies⁶ who also knew the Montagnais-Naskapi well:

"Depending solely on the chase for a subsistence, they of course, lead an erratic life, following the deer⁷ in their migrations from place to place; keeping generally together in large camps, a circumstance that frequently subjects them to the extremes of starvation; the game being soon destroyed, or driven to a distance from them—in this respect they differ from their neighbors the mountaineer Indians, who seldom or ever hunt together in large numbers, two families generally associating themselves for that purpose. . . . They are extremely liberal toward each other; whatever the hunter brings to camp is shared without reserve, in equal proportions among the whole community—this custom is not peculiar to them however, they possess it in common with all Indians who live by the chase. They are not fur hunters, nor is the mode of life they lead favorable to it; the chase of the deer leads them to the barren parts of the country, while the fur-bearing animals are only to be found in the woods; moreover, their favourite occupation furnishes them with all they require—they clothe themselves with deerskins—their tents are made of the same material, as well as their nets. . . . Their number is but small, 40 or 50 families comprise the total of those frequenting the posts of Ungava Bay."

In the preceding statements the habit observed among the northern and eastern bands of the

³ The several grants of the Faculty Research Fund of the University of Pennsylvania from 1931 to 1933 have made it possible for Dr. A. I. Hallowell to carry out his expeditions in the field among Cree and Saulteaux, and for Speck to add to his earlier field notes obtained from the Montagnais of Lake St. John and surrounding bands accessible through them. Again in 1935 another grant (no. 286) by the same committee made possible a return to the bands of the southeastern coast as far as Eskimo River in the Straits of Belle Isle. Additions were then made to the material previously collected.

⁴ This point has been approached in several previous statements, and Dr. D. S. Davidson has also used the same line of view.

⁵ Abbé N. Caron, "Deux Voyages sur le St. Maurice." *Trois-Rivières*, 1887-8, p. 128.

⁶ Davies, W. H. A., "Notes on Ungava Bay," *Transactions of Literary and Historical Society of Quebec*, Vol. IV, pt. II, 1854, pp. 129-131.

⁷ By "deer" Davies means caribou.

Montagnais-Naskapi, of starting the fall migration into the interior hunting grounds in a group hunting communally is brought out in clear terms. These bands remain in this type of social formation as long as game conditions permit, that is to say as long as the caribou can be followed and killed in sufficient quantity to support them. Should the caribou fail them, however, they are obliged to separate into small parties to save their lives and fall back upon the hunting of small game wherever they can find it for the remainder of the season. This means that they break up into family units comprising the man of the family, his wife, children and such dependents as he may have. The family group of this designation may also include his son or sons and their wives, or his daughters and their husbands, according to whether their residence is patrilocal or matrilocal. The latter circumstance raises a point of no little importance in the history of band affiliation among the northern tribes, one which Dr. Hallowell is weighing out in its bearing, likewise, upon marriage procedure.

It seems conclusive from the data at hand, then, that stress-conditions govern the breaking up of the communally hunting band into family units. And stress-conditions arise through the movements of the game. Thus the ruling element in the problems the natives of the northern districts have to face is the success or failure of the hunt for the Barren Ground caribou.

Matters are quite different in the economic circumstances of the bands of the southern and western portions of the Montagnais-Naskapi habitat, where the hunting environment is that of the forest, where game is more diversified and more abundant though smaller in size, and scattered through the forests. And here furthermore the moose enters into the economic system while the caribou is of the woodland race which runs in smaller numbers.

In the environment of the northern bands the struggle for existence is intensified by absence of forest, causing a less thorough dispersion of the game and a difference in its type. We hardly need attempt to outline the effect of the forest-covered hills mountains and swamps upon the life of animals and their distribution over territory, as contrasted with the conditions prevailing in the thinly forested or treeless tundra farther north. The animal life of the open regions is wide-ranging and mobile.⁸ Hence the northern

bands hunt in a horde formation, as do the wolves, in pursuit of the caribou which travel in hordes and upon which they depend so largely. The frontier dividing the tundra from the forest, to be concise, is the factor determining the character of animal life and the social-economic life of the Indians within and without these respective zones.

The question of change and decline in population of the bands under consideration, and in fact those of the Labrador Peninsula at large, has engaged the attention of statisticians of population, government officials, missionaries, traders and the Indians themselves for a long time. Speck commented upon some of the figures available from several earlier and later sources in a paper to which reference has previously been made. Taking the collective estimates of the population of the bands under consideration in this report, we have a total of 300 souls listed for Seven Islands in 1857, while the census of Indians in Canada of 1924 gave 380 for the same agency. The matter has much deeper implications than the mere question of survival, in the relationship between mortality among the natives, the rise and fall of populations in the different bands and the still little-known periodic cycles of abundance of animals; the so-called seven-year "plagues" affecting the animal population of the northern regions.

Seton and others have drawn attention to these problems. Elton, in a work which deserves the careful attention of anthropologists, gives considerable space to faunal fluctuation and migration in the Labradorean area.⁹ He shows how an increase of mice, or even mosquitoes may affect, sometimes through a long chain of events, the movements of caribou, and hence the fortunes of man. He maintains that "there is hardly a single fur-bearing animal in Canada that does not fluctuate in numbers from year to year in a most striking way."¹⁰

Burt, in a recent paper,¹¹ makes some valuable

Dymond, for example, indicates that both the white-tailed deer and moose may absent themselves from considerable areas over long periods of time, and then again return. See J. R. Dymond and L. Snyder, "The Faunal Investigation of Lake Nipigon Region, Ontario," *Transactions of the Royal Canadian Institute*, Vol. 16, 1928, p. 247.

⁹ Elton, Charles, *Animal Ecology and Evolution*, Oxford Press, London, 1930, pp. 18-23, 30-31, 40-42, 78. See also Murphy, R. C., "Conservation and Scientific Forecast," *Science*, n.s. Vol. 93, pp. 605-607, 1941.

¹⁰ *Ibid.*, p. 18-19.

¹¹ Burt, Wm. H., "Territorial Behavior and Populations of Some Small Mammals in Southern Michigan," *Miscel-*

⁸ Even the herbivores of the forest zone may not constitute an entirely static and reliable quantity. J. R.

observations on the size of the home range of certain of the smaller northern mammals, as well as pointing out many gaps in our knowledge of territorial range, particularly among the larger forms. He makes it clear, however, that the smaller fur-bearers are very limited in their range of movement under normal circumstances. The size of the area occupied by an animal is necessarily limited by the creature's ability to travel and its needs in terms of food and protection. Predators will tend to range more extensively. A rodent, ever in danger from enemies, must be thoroughly familiar with the area over which it ranges in order to survive. In Burt's own words "Animals that are moving about in search of a place to claim as their own are covering unfamiliar territory and are much more vulnerable . . . than are those in established territories."

Having noted these observations of Elton and Burt let us consider them in terms of their possible influence upon the hunting pattern of man. Elton has considered the tremendous fluctuation in numbers and area of movement of some of the northern animals. The significance of this to a hunting people is tremendous. In the course of his discussion Elton makes one statement of profound interest to the ethnologist: namely, *that the beaver is almost the sole northern fur-bearing animal the numbers of which have not been observed to fluctuate with the unsteady cyclic variability to be found among other northern forms of life.* The beaver, it must be remembered, was food long before he represented other forms of wealth. It now seems evident from these biological observations that he was a most reliable and steady source as well.

Consider further the comments of Burt upon the relatively small range of the rodents in general. The beaver has little chance to survive among fierce and powerful predators, such as the lynx and glutton, unless deep water is available as a retreat. They are thus, in the words of another zoölogist, "restricted to the water courses, reveal their presence by unmistakable signs, and build domiciles such as their lodges, which, though not furnishing exact information as to the number inhabiting them, are at least conspicuous indicators of family establishments. . . ." ¹²

In other words, as the writers maintained in a previous paper,¹³ an animal of great significance economically, even before white contact, is seen to be one the habits of which make it easily located even under arduous winter conditions, the range of which is limited, the stable home habits of which make it possible to husband by restraint in killing, and the need of proper stream conditions of which again foster a limitation of sites sufficient under scarcity to place a premium upon assured family ownership. Moreover, such an animal, dependent to a major extent upon aspen bark¹⁴ is preëminently a creature of the forest and not the tundra zone. When its seeming freedom from cyclic instability is taken into account its human importance is accentuated. We are greatly in need, however, of a more detailed knowledge of the animal and human interrelationships of the whole Canadian region.¹⁵ An approach to this aspect of the dove-tailing cycles of human and animal fluctuations in number will be a future step in the method of treatment of the economic problems of the area, under ecological methods.

Later, when the present collections of data shall have become records of a faded past era, we shall have to use them as we now use material placed on record, scanty as it may be, by investigators whose labors date back twenty years or more. The collections of matter offered in the pages to follow are accordingly enhanced by a time perspective now of almost a generation of age, since they represent conditions prevailing in family and band history between 1915 and 1925. Had we a record of affairs in these groups characteristic of the period say about 1900 and again

Bulletin, Syracuse University Publications, Vol. 4, No. 4, 1927, p. 576.

¹³ F. G. Speck and L. C. Eiseley, "Significance of Hunting Territory Systems of the Algonkian in Social Theory," *American Anthropologist*, Vol. 41, No. 2, April-June, 1939, pp. 269-280. Most recently Hunt (G. T. Hunt, *The Wars of the Iroquois*, University of Wisconsin Press, Madison, 1940) emphasizes the influences of the fur trade, especially the beaver trade, in causing aggressions of the Iroquois into the territories of the Algonkian.

¹⁴ Warren, Edward R., *The Beaver*, monograph, American Society of Mammalogists, Williams & Wilkins, Baltimore, 1927, p. 17.

¹⁵ Klugh, A. B., and McDougall, E. G., "The Faunal Areas of Canada," *Handbook of Canada*, University of Toronto Press, 1924, p. 202. "The difficulty of dealing with the faunal areas of Canada is greatly increased by the fact that data on the distribution of the animal life of the dominion is, as yet, very incomplete. There is not a single locality the whole fauna of which is known."

laneous Publications, Museum of Zoölogy, University of Michigan, No. 45, May 8, 1940.

¹² Johnson, Charles E., "The Beaver in the Adirondacks: Its Economics and Natural History," *Roosevelt Wild Life*

of 1880, the time perspective so much needed to demonstrate the change processes of the hunting societies could be visioned. Our first era of ethnological observation, however, must begin with that described here. The next is about now due after a lapse of nearly a generation of hunters' lives. It is then a happy thought that the material of the accompanying report concludes nothing, but on the other hand begins something which is now ripe to be reharvested by newer and better understanding and method.

FORMER COAST DIVISIONS

That there was in former times a more or less permanent population resident on the immediate coast of the St. Lawrence is clearly shown in the early accounts. These refer to Tadousac and Seven Islands as centers of the Montagnais contacts from 1673 onward. We learn of this from numerous sources. In a letter attributed to a missionary of the Saguenay in 1720 appears the statement that Tadousac has been for a long time the gathering place for all the Indian natives of the north and the east.¹⁶ Crépéul (1673-4), the Jesuit, gives a report on the natives of Seven Islands and Tadousac which were then centers of congregation for the coast Indians and those who emerged to trade and associate with their kind from the interior.

These groups, if they ever possessed an independent character, separate from their relatives who migrated annually from the hinterland then as they do now, have left no indication of their social composition lasting down to the present. Perhaps if they were originally band units they have in the course of time become entirely fused with the larger migrant bands, the former coast-dwellers from Tadousac to Seven Islands. The natives themselves are aware of the two populations, one holding to the coast, the other dwelling in the interior. These are respectively denoted *notci-mi-wilnu'ts*, "people of the interior," and *wi-ni-pe'gwilnu'ts*, "people of the salt-water." In another paper, comment has been offered upon the significance of these terms.¹⁷

A casual observer could well imagine the coast-dwelling populations to enjoy economic ad-

vantages superior to those of the inland hunters, assuming that the more abundant resources of the bays and gulf would provide a richer subsistence. This does not, however, seem to be the case. Any of the coast "métis," of the "petite chasse," would exchange his "job" for the life and fare of the "gros chasseur" of the far bush. He invariably does so when his vigor and fortitude secure for him an offer from a big hunter in need of a partner. For the "métis" it would mean escape from the precarious employment of a small sphere to the freedom, the adventure and possible greater profit of furs of the big woods. The coastal natives are by-and-large the "petites gens," the physically incapacitated, the near-bankrupt, the lazy, the indigent, the timid. One might also imagine the coastal families to claim prestige through their assimilation of white mores. But they could not assume it in the presence of the interior hunters. Prestige lies with the latter, socially and financially, as observed by Speck between 1915 and 1925.

Without pretending to solve the question presented by the confusion of testimony on the earlier history of these long-dissolved band groupings, it is now evident that the two bands, Ste. Marguerite and Moisie, which hunt and trap over the territories in question, have become amalgamated. Some of the details referring to the earlier natives of the coast districts will be taken up under the headings which treat of these two groups.

It is true at the present time that a strip of country bordering the Gulf is not regularly inhabited or worked for its fur and meat by any specific family tenants. According to the lay of the coast, its rock exposure, and scarcity of wood, the distances of the worked hunting ground may be as much as forty to fifty miles inland. For the most part these stretches are exploited for what natural resources they may yield by certain families which remain permanently in the neighborhood of the trading posts and fishing settlements. Most of them are of mixed blood. Their connections, along both social and occupational lines are with the posts. Routine follows the callings of the coast. In summer off-shore fishing in boats, filling various capacities in affairs between the posts and the hunters from the interior with their booty of furs when the exodus to the coast is on, taking employment from the settlers also to fill in time, in the fall hunting and netting seals, in the winter taking small game and fur wherever it can be found

¹⁶ Rapport des Missions du Diocèse de Québec 1864, pp. 21-2, see A. E. Jones, S. J., *Mission du Saguenay*, Relation Inédite du R. P. Pierre Laure, S. J. 1720 à 1730, Documents Rare ou Inédites, Montreal, 1889, pp. 4-5. Also Jesuit Relations, vols. 54, 63 and 65.

¹⁷ F. G. Speck, "Montagnais-Naskapi Bands and Early Eskimo Distribution in the Labrador Peninsula," *American Anthropologist*, Vol. 33, No. 5, 1931, p. 580.

pieced out again with employment from the posts, in the spring fowling and sealing until fishing opens up. We are at a loss to conclude the extent to which these pursuits would coincide with the economic cycle of an aboriginal population in their direct line of ancestry. It is possible that from early times there were subdivisions of the "Montagnais" who consistently clung to the coast in contradistinction to their higher-altitude-loving kindred, the so-called "Naskapi" of the hinterland. Yet one has the feeling all the while that their conditions have been considerably moulded by association with Europeans since the early establishment of the French fishing stations. Certain it is that assimilation with inhabitants of the latter has progressed to a degree necessary to be given full weight in the story of composition of the coasters.

Localities along the coast are, however, well known even by those whose permanent homes are strictly inland. The islands forming the Seven Islands group are enumerated by Sylvestre Mackenzie, chief of the Michikamau band and elected head man of the aggregation of groups at Seven Islands (1925). They were given as follows:

Kaictabo' ministu'k, "Big Island," Grosse Boule.
Acini'uts'wap ministu'k, "Stone House
Island,"¹⁸ Grande Basque.

Kawaba'pickats ministu'k, "White Rock
Island."

Backwo' ministu'k, "Basque Island," Grande
Basque.

Mənwani's, "Little Island," Manowin.

In view of what has been said regarding the unassigned coastal zone, a section representing this strip has been left unmarked by boundaries of the bands when shown on the chart. It would also represent the recession of the Indians who live by hunting from the coastal margin of the peninsula, due to the disappearance of the game there resulting from the establishment of French-Canadian fishing stations at the mouths of rivers. In this connection the following faunal references from the Jesuit Relations¹⁹ are of interest:

The first is a memorandum for a missionary to be sent to Seven Islands:

"He will find there next spring at various times about 150 persons, both adults and chil-

dren. He will probably see all these—and perhaps others who come from the interior or *from the shore of the sea.*" (Italics ours.)

"The entire coast is of frightful aspect. There is not even the space of a drying ground of soil; it is all rocks, covered with very small trees of spruce and fir;—save the little birch, not one beautiful tree. There is no end to game, all marine birds. . . ."

"All along the coast, seals are to be seen, upon which the savages live during the entire summer."

Hind also yields interesting material on the coast division:

"When leaving the coast for the interior, many families have particular rivers to go up by, and often in a large body; but once a certain distance inland, the whole party break up and disperse into bands of two and three families each to pass the winter, and seldom see each other any more until spring; but before taking their final leave of each other a place is appointed to meet, and he or they who first arrive at the prescribed rendezvous (if having sufficient food to wait) keep about the vicinity until the whole party collect; they then go to fetch their canoes, wherever left when the cold sets in, and employ themselves, some in making new canoes others in repairing the old ones, until such time as the ice breaks up in the large lakes, and the waters subside in the rivers; they then move off in a fleet of canoes towards the sea, and generally make their appearance at the coast about the latter end of June."²⁰

The fact that the location of these bands in the seventeenth century lay at the frontier of distribution of the Eskimo westward in the peninsula gives them a tinge of importance. While at present we do not know what the force of this circumstance may have been upon both groups it is, nevertheless, a circumstance to be borne in mind. A series of sources available for this distribution terminus of Eskimo has been collected and cited in the article quoted previously and to which we would now refer again.²¹ Another extract from Hind (1853) which bears directly upon the Indians of the Moisie and their traditional conflicts with Eskimo presents material worth quoting:

¹⁸ Hind, H. Y., *Explorations in the Labrador Peninsula*, Vol. II, 1853, p. 121, quoting a Wm. Chisholm who lived for forty years among the Montagnais as a factor of the Hudson's Bay Company.

²¹ Speck, *op. cit.*, 1931, pp. 564-71.

¹⁹ The informant stated that a stone house had once been built here by the government, whence the name.

²⁰ *The Jesuit Relations*, Thwaites edition, 1899, Vol. 59 pp. 57-59.

"The mouth of the Moisie or Mis-te-shipu' River—the 'Great River' of the Montagnais Indians—enters the Gulf of St. Lawrence in longitude 66° 10', about eighteen miles east of the Bay of Seven Islands, and has its source in some of the lakes and swamps of the high table land of Eastern Canada. For centuries it has been one of the leading lines of communication from the interior to the coast, traveled by the Montagnais during the time when they were a numerous and powerful people, capable of assembling upwards of 'a thousand warriors' to repel the invasion of the Esquimaux, who were accustomed to hunt for a few weeks during the summer months a short distance up the rivers east of the Moisie, as they do now on the Coppermine, Anderson's and Mackenzie's Rivers, in the country of the Hare Indians and the Loucheux. The old and well-worn portage paths, round falls and rapids and over precipitous mountains on the Upper Moisie, testify to the antiquity of the route, independently of the traditions of the Indians who now hunt on this river and on the table land to which it is the highway.²²

MOISIE AND PETISIKAPAU BANDS

There is some evidence to show that at a former period the families who dwelt in the region of Petisikapau Lake constituted a group about as well defined socially and economically as the other family consolidations which have been classified as bands by both Indians and whites. Through changes affecting the composition of the older units of the remote interior in the century past it seems that the Petisikapau horde has suffered a fate similar to that of the Kaniapiskau and Nichikun people recently, and which is overtaking the Michikamau group at the time of writing. The disintegration of the band has thrown its members into the population complex to the southward, nearer the shore-folk who make rendezvous at the Seven Islands post. Since the hunters from the Petisikapau endroits descend by way of Moisie River and associate with the people deriving their identity from the Moisie, they have become considerably fused and intermarried with this group. The Moisie Band derives its name from the river of the same name, which denotes its muddiness. The native proper name is, however, *Mictaci'pu*, "Big River."

The Indian family names of the preceding generations have been superseded. French sur-

names of the families which operate territories on the lower Moisie River indicate what has transpired in their history; extensive intermarriage with the French-Canadians of Côte du Nord, as the north shore of the St. Lawrence is politically and geographically designated.²³ Most of them show the mixture in some degree. They are bilingual for the most part. Some of the younger men will take employment, when it is possible, with the traders, prospectors, hunters, and lumber concerns, temporarily, as a form of economic relief if not of progress in the way of civilization.

Concerning the location and ethnic constitution of the Moisie Band, we quote from Speck:²⁴

"Like the Ste. Marguerite band, the Moisie people seem to be of mixed extraction so far as original units are concerned. The families who operate nearer the coast may be the residue of a population of former times which belonged south of the Height of Land, and the northern families of those belonging in the interior. Whatever may be the explanation of the somewhat confused condition of affairs now it is fairly certain, from native sources of information, that it has not undergone extensive change within the last two generations. The families falling under this band classification number ten, and hunt and trap the territory up Moisie River and east of it to Mingan and Attikonak lakes, from the coast to the headwaters of Hamilton River beyond the Height of Land.²⁵ Also like the Ste. Marguerite Indians the majority of the families operate south of the divide, have smaller hunting grounds, and observe more closely the family system. The northern families seem to have connections with the limited nomads of the interior lake country whose populations have in

²² Photographs of nearly all the adults of the group were made and the films are filed in the collections of the Museum of the American Indian (Heye Foundation, N. Y.).

²³ *Op. cit.*, pp. 584-585.

²⁴ These districts were located on the chart published in 1913 by Gustave Rinfret, *Département des Terres et Forêts, Québec, 1913*, by finger of the men of the band who gathered to contribute to the investigation. Inexactitude was inevitable. Yet on the whole it was apparent to Speck that these hunters were not conscious of boundaries to any degree comparable with the land division sense of members of other bands investigated by him in regions where the limitations, both geographical and social, were more closely observed in native life. This condition was apparently due to a less distinct pattern of land proprietorship in the area of the eastern Montagnais-Naskapi. The marginal situation of these groups from the point of view of the communal versus segregated family methods of pursuit would seem to be a part of the question.

²⁵ Hind, H. Y., *op. cit.*, Vol. I, pp. 9-10.

recent years become so dispersed. Upon the closing of the Hudson Bay Company's post at the mouth of Moisie River the band transferred its summer mission and trading center to Seven Islands. It has now (since 1915) no separate chief.

"In Hind's time (1861) the hunters from Ashwanipi Lake were referred to as the 'Aswanipi' band, which he says was dispersed in the nineteenth century to the north and east. This lake is now hunted by families which come under the name of the Moisie group who may have pushed northward since that time."

Speck's investigations yield the following data on the ten families, previously referred to, who make up the Moisie band:

1. Ange Picard hunts and traps in a small way from the falls of Moisie River upward for about 40 miles on both sides of the Moisie. The district is an unproductive one, from which the great game has been banished by increase in the coastal populations. With him as partner is Joseph Vollant, who has recently been so seriously disabled by an injury that he is an object of local charity. Both have mixed families of young children.

2. Philip and Tommy Moise (brothers), also Moise Vollant, use trapping grounds on both sides of Moisie River for about 30 miles above the forks of Moisie. These families are of mixed Indian and French extraction. Owing to conditions of sickness in the band at the time when their members were contacted the desired details of family make-up were not obtained.

3. Bernard Pinette operates in a territory beginning about 40 miles above the forks. His father, Bastian Pinette, from whom he takes his land, is now too old to hunt, and stays at the village of Moisie.

4. Magloire Regis has a location on Manitou River extending to Mingan Lake, some thirty miles inland, and east of the family heads thus far listed in this band. Magloire is brother to the ex-chief, George Regis (No. 5) of the Moisie band. In this direction we have an approach to the people of the Mingan Band. The latter has not been made an object of attention so far in the contemporary survey of the peninsula. We have no data on the composition of the family.

5. George and Delphis Regis (brothers) pursue their trapping and hunting each winter on both shores of Moisie River about 60 miles from the mouth. Information is lacking concerning their children. George Regis held the office of elec-

tive chief of the Moisie Band prior to 1922, representing the combined populations of the Indians from various bands assembling at Seven Islands. He was succeeded by Joseph Vachon (No. 10, Ste. Marguerite Band).

6. Johnny, Joseph, Charles, and George Vollant, brothers, cooperate in trapping and winter residence over a tract lying about the foot of Kaopasho Lake (*kaopa'co*, "narrow passage in middle") and headwaters of the Moisie, northeast branch. The informants who indicated their holdings on the chart included a lake to the northeast just below the Height of Land as an extension of their working area. This tract was inherited from their father, old Malek Vollant, who is now too old to make the peregrinations to and from the interior to the coast. He stays at the Seven Islands post.

7. John Marie Rock (*Djama'ni*, Indianized from the Christian names) and his son of the same name with wife, comprise a two-hunter partnership in a fairly large district about the Height of Land east of Kaopasho. Mamickau ("northeast") is the lake near their geographical center. It might be thought that the name Rock is a translation of *A'cini* "rock," a family name among the St. Augustin Indians far to the eastward on the Gulf, but it is not so considered, being ascribed, rather, to French origin (Rocque).

8. Charles Pilo's sons, Mili', François, and Sylvestre, congregate upon grounds lying at the head of Kaopasho Lake, on both sides, and northward into Ashwanipi Lake territory a little across the Height of Land, according to their indications on the work map used in the listing. No further information was recorded of their families. They held possession of the region from their father Charles, and trap in subdivisions of the grounds agreed to among themselves.

9. François Jérôme and his dependents comprise the family group which winters on the north (lower) sides of Ashwanipi Lake. Further information is wanting.

10. Tommy Vollant, a member of the family of the same name (No. 6) localized on lower Kaopasho Lake, has extended his hunting and trapping routes to the northeast beyond the Height of Land covering the watershed of a series of large lakes around and west of Attikonak and Ossakmanouan lakes. These vast and barren stretches of plateau desert demand mobile habits of their human dwellers and closer boundary determinations are impossible to consider. We are led to conclude that the populations here live

and move more in a concourse than those of more abundant natural zones.

The families of Moisie classification so far enumerated are less restricted in their manner of hunting and trapping than those to the southwest toward Lake St. John, for instance. The scarcity of edible large game animals, the devastation of the region by annual bush fires, not to mention the growing encroachment of Canadian-French trappers in the European drift northward to exploit new areas, is having a destructive effect upon their game resources. Reactions upon the human inhabitants, who for so long have lived in relative equi-balance in these deserts, have been noteworthy destructive in the long run.

PETISIKAPAU

The Petisikapau people, who, as we have already observed, have disappeared as a major and geographically independent group into the limbo of association with the Moisie Indians, derive their name from the lake of their ancient location, Petisika'pau. The term *pe'tasaga'pao* defines a body of water "narrowed in the middle," which seems admirably appropriate for its shore contour. The lake is noteworthy for having been the location of an early interior trading post, Fort Nascaupé of the Hudson's Bay Company founded in 1840, for commerce with the remote bands of the hinterland.

"The information upon which this and the following band are classified is extremely little," Speck records.²⁶ "There seems," he says, "to be an area of several hundred miles, according to Low, with a very sparse population. And from testimony obtained from natives at Seven Islands his claim is borne out, although a few of them from these endroits, east of Lake Michikamau north to the Kaniapiskau River, gave their identity as Petisikapau people and were so recognized by the others. My listing assigns six family heads to this group. I would not, however, insist upon separate classification as a band for these families, although they are listed as such for the present. The vagrancy of the hunters of this central region is a noteworthy feature of their lives, to which we may add the decrease of its population as causes contributing to the uncertain identity of its few remaining families. Both of these bands, if such they are, pursue the winter hunt for meat and caribou in collective groups. Hind refers in several places

to 'Naskapi' from this lake and mentions a Petisikapau band of fourteen families, which has induced me to consider its classification as a band unit of the past if hardly one of the present.

"By the Indians at Seven Islands the name *Mone'yik wilnu'ts*, 'white spruce people,' is also applied to the inhabitants of Menihék Lake, a branch of Petisikapau, though I do not know how to discriminate between the two as band names. Were the records of old Fort Nascaupé, founded on Lake Petisikapau in 1840 and long since abandoned, available, some light might be thrown upon the affiliations of the natives by tracing their family names."

That the Indians constituting the Petisikapau band of former times have, since the time of Hind (1861), also become assimilated with those who then constituted the populations nearer the coast at Seven Islands is indicated by Hind's notes. He stated that the Petisikapau band then comprised 14 families.²⁷ We could not (1922-5) designate the few families who winter as far in the interior as the said lake under the caption of a distinct Petisikapau band apart from their co-residence and intermarriage with the coastal units about Seven Islands. A similar dissolution has been the fate of the band which Hind informs us to have been formerly located at Ashwanipi Lake but dispersed to the north and east in the 19th century, and which he designates as the "Aswanipi" Indians. The judgment of the hunters with whom the matter was discussed at Seven Islands was that the old Ashwanipi units had merged with coastal branches into the Moisie band. As such they will be considered in another section of this paper.

These observations concerning the remote families who winter in the high lake districts of the remote interior plateau are to be taken as founded upon the testimony vouchsafed by the heads of the same name-families with whom the matter was discussed at Seven Islands and checked with the statements of Henry Hind who sojourned with them eighty years ago. As our information stands it seems that the absorption of the interior bands into the coastal populations began with the movement of the Ashwanipi horde in the mid 19th century, joining with others to form the Moisie Band of later times, followed by the merging of the Petisikapau and Kaniapiskau families with these of the Ste. Marguerite Band, and lastly the dispersion of the Nichikun people to join temporarily with the

²⁶ Speck, *op. cit.*, p. 590.

²⁷ Hind, *op. cit.*, Vol. 1, p. 82.

general populations of the coast at Seven Islands. The Michikamau group it seems has withstood the tendency to break up better than the others.

As testimony of movements of this nature, we have mention by Hind²⁸ of a Naskapi hunter named Paytabais who had starved to death in the interior about 1857. This man, we are told, lived about old "Fort Nascopie." At the present time a man named Petabesh (*Peta'bec*) comes down to the Seven Islands post with the families from far inland, whether from Petisikapau or Michikamau it was not ascertained positively. It is likely that he carries the family surname first noted by Hind.

Old Napes Gregoine (*Gne'gwen*, Indianized French, Grégoire) and his son Napes, represent a family for which the information obtained was very unsatisfactory and confused. The upper environs of Menihék Lake down northward to Petisikapau, and embracing the area of *wulce'gocipu*, "otter river" (unlocated on the charts) were given by several men of this name as the ancestral domains. The family was evidently dominant in the Petisikapau group of almost a century ago, having since merged with the Ste. Marguerite band in part. (See Ste. Marguerite, Nos. 5 and 6.)

Nabesh Gregwenish (*Gnegweni'c*, "Little Gregwen") was given by informants as the hereditary hunter and trapper of a large area on lower Menihék and Petisikapau lakes. He is married to a daughter of Sylvestre Mackenzie, head man of the Michikamau group, and is closely associated with his father-in-law. No specific data on the family composition of these men were secured.

It should be noted here that the families who were centralized about Menihék Lake bore a distinctive name, if they lacked a separate classification, among the Indians at Seven Islands. The name *Mone'yik wilnu'ts* (or *i'nu't'*) "white spruce people," was current, derived from the lake in question. It was not, however, thought to be specific enough to classify them as forming a distinct band, for which reason, at the time, their little understood associations were left open. Disintegration of the older interior hordes has left a chaos of identity in the subsequent groupings of these families.

Michèle Ambroise and his son Joseph, about 20 years old, hunted the environs of Petisikapau Lake from the shores northeast for a distance of some 70 miles. Since Michèle's death within

the last few years his widow and son continue the work. Hind (1863)²⁹ mentions a hunter from the interior as Ambrosis, who held grounds at that time, about Nipisis Lake (Moisie Band No. 3), a body of water lying not more than about 60 miles inland from the coast. Ambrosis answers to a diminutive form of the name Ambroise, yet there is little more to identify these men as of one line of the same family in view of the distance separating the hunting grounds noted for them.

Louis Michèle. The records of the Moisie hunters include him as working a territory on Moisie river, aided by a young man, Pierre Dominique, 20 years old. But no further data on the relationships of these men are at hand.

STE. MARGUERITE AND KANIAPISKAU BANDS

The Ste. Marguerite River is on one of the large and important streams draining the south central slopes of the peninsula and emptying into the Gulf of St. Lawrence a few miles west of Seven Islands Bay. It is called *Tcema'n'bi'ctuk*, meaning "River Parallel with Hills." The band that is allocated upon its waters bears the name *Tcema'n' bi'ctukwilnu'ts'*, "River Parallel with Hills People." The band seems to have been one of old formation for we have mention of some of the families in Hind's narrative.³⁰ The ten families at the present time forming this group contain some old patronyms. A few notes concerning its habits will serve to bring out some characteristics.

Seven Islands Bay has been continuously the summer rendezvous of the band, in fact its exclusive resort until the movement began a generation ago for the hunters of the Moisie band to move over and spend part of their summer period with the Ste. Marguerite people. Even now the social monopoly of the Seven Islands trading post and mission rests in the hands of the Ste. Marguerite Indians. One part of the village is their quarter, the other houses remaining vacant until the families from Moisie have come to occupy them as they do late in July, during the last two weeks of the mission held annually for the natives of the combined bands of this section of the coast.

A very close connection exists between the Ste. Marguerite Indians and the Kaniapiskau families immediately north of them. There

²⁸ Hind, *op. cit.*, Vol. I, p. 188.

³⁰ Hind, *op. cit.*, Vol. I, p. 11 gives the same name (Ichimanipistuk) for the Ste. Marguerite in 1861.

²⁹ Hind, *op. cit.*, Vol. I, p. 15.

would, indeed, be little reason to separate them were it not for their habit of using different local names for their groups and for the rather vague geographical boundaries that separate them.

These two divisions may possibly turn out to be divisions in name only when more is known of their former history. It would be necessary to know, for such a decision, just where the grandfather of the present elder generation of the Tcelnish families had his location in the interior. At this present period of time, the three family units of the name draw their sustenance from hunting districts far beyond the height of land in the Lake Kaniapiskau region, while only one having the Tcelnic patronym (*i.e.*, Alexandre) hunts south of the divide. It might be thought that a century ago the hunting would have been better nearer the St. Lawrence coast; hence a withdrawal of the old families toward the interior plateau with the retreat of the game in the same direction. This circumstance would, however, apply chiefly to the caribou. If we were to seek to connect the earlier story of the Tcelnic family name with similar patronyms elsewhere in the Naskapi territories we should be led afar since the same name occurs in several directions among the bands as far west, for instance, as Lake St. John.

Hind who knew this band fairly well in 1861, says that the first migration of the families from the interior to Seven Islands was two years before his visit there, bringing it in 1859.³¹ He mentions the family name of Tcelnic (Chelneesh), and Otelne as being those of interior or proper Naskapi derivation.

Things have not changed so much in regard to location of bands and their movements in assembling at the Seven Islands post and mission since Hind's time (1861). The Ste. Marguerite band, which he referred to as Montagnais, then being as sharply defined from those he called Naskapi inhabiting the Moisie as far as Ashwanipi and Petisikapau as they are now.

The Kaniapiskau people are known among their confreres by the name of the lake (*Kaniapiskau*, "Rocky point"), which has for many generations been the pivotal center of their winter wanderings. A few notations we possess concerning them specifically may be summarized from the report of Speck in 1931:³²

"The identity of this band, like that of the preceding, is known only on the authority of

hunters from the region who were encountered and questioned upon the occasion of their annual migration to the post at Seven Islands. When questioned as to their affiliations they used the name given above, but it does not seem that there is much political consciousness to the few who answered to the classification. Low refers to Indians trading at Nichikun post who hunt about Kaniapiskau and down its discharge about fifty miles, but speaks of uninhabited areas between here and the western boundaries of the Indians from the Northwest River, and another such on both sides of Koksoak River from the Nichikun territories to where those of the Ungava hunters begin."

Again, investigations by Speck furnish data concerning members of the band:

1. Sylvestre Tcelnish hunts with his son Bastian. Bastian had six or seven children in all—two little boys between 8 and 12, a girl about 17, the rest younger. Since by his own declaration he had "too many mouths to feed" through hunting alone, he (Sylvestre) lured Tommy Jourdain to help him feed his family. Tommy, although a "son of a bitch of a good hunter" is a consumptive, but it is expected that he will marry Bastian's daughter. Tommy is a grandson of old Charles Jourdain. The men themselves furnished the data on this tract, the most northerly of which Speck obtained data. It lies northwest of Lake Kaniapiskau down Kaniapiskau River to Big Otter River to within about 50 miles of the big bend of the river and 200 miles from Fort Chimo.

2. Pierre (also Pielis) Tcelnish (*micienat'e'o*, "great approacher of game") is the last of his paternal line, and is related to the family mentioned above. He hunts with his son, Shimun Piel (Simon Peter), about 16, who does a man's work on the hunt and trap line with his father. They hunt the environs of *Packwule'o cakh'i'gan*, "fire lake," and *Gawace'gemat*. These waters lie southeast of Kaniapiskau Lake, and also just west of the lake, lying about 300 miles up the river from Seven Islands.

3. John Pierre (originally of the Ungava Band) married a daughter of Sylvestre Tcelnish, now hunts on grounds formerly held by Otelne, now deceased. (This territory was possibly allotted due to circumstances of family No. 1. It has not been inherited.)

4. Alexandre Tcelnish hunts with two grown sons, one married and one with a child. His grounds extend westward from Ste. Marguerite

³¹ Hind, Vol. I, p. 4.

³² Speck, *op. cit.*, pp. 590-591.

River at Rivière à la Bataille (about 51° 40') and Portage de Manicouagan (which is the route to Manicouagan River some 60 miles distant about 40 miles west, i.e. over half way to Lake Tschimanicouagan on the Manicouagan.

5. Napeo Gregoire (Gnegwen), 40 years old, with two sons and two daughters, hunts between Ste. Marguerite River and Lake Aswanipi. This hunter and his family bear a low reputation among the men of the band for violating the credit allowances made by the post factor in advance of the winter hunt. The practice is deplored by the other members of the group as damaging the interests of them all in financial transactions with the factor. The older generation of this family is listed with the group or band wintering in the distant territories of Petisikapau and Michikamau lakes. The family surname may be identified with these far northern hordes. The confusion of first names and family names in the Gregoire line leaves us in a position which becomes most difficult to clear up.

6. François Gregoire and his two sons, Nabeo (married, with no children as yet) and Antoine (24 years old) hunt west of Ashwanipi lake and south of the Height of Land working the environs of two lakes still unmarked on the charts available, namely Chibougamou and Wabushkatso ("hare excrement"). Their next neighbor on the north was stated to be Nabesh Gregoire, a close relative. (The synonymy of family and personal names here again causes considerable confusion of identity.)

7. Tomah (Tamas) Otelne, "Tongue," is an old man 60 years of age, disabled through the loss of an eye, and retired from active hunting and trapping. He and his brother Nisham Tomah (Otelne) who died about 1923 (at the age of about 50) hunted together through life a tract on Manicouagan river (*mānikwa'ganictu'k*) about 60 miles long and 40 wide on both sides. It required about a month's travel, he stated, to reach the endroits from Seven Islands. He and his brother hunted the same territory worked by their father, and they thought the same held in the paternal line for generations back. He had had no daughters but four sons, with only one—Nabes Otelne—surviving, who operated with him until his death (1923). Nabes was known as a famous hunter by the factors of the Seven Islands Hudson's Bay Company Post. Philip (aged 21, and just married at the time these data were secured in 1923) will succeed to the paternal hunting district from now on, taking up his first

regular hunt in this year. This terminates the male lineage of a famous and estimable line of hunters who had operated the same territory in male succession for at least four generations.

The character and personality as well as the hunting endroits of a Naskapi named Otelne are made the subject of some treatment by Hind. He leaves us in a difficulty, however, to explain the present hunting locations of the family to the westward of Ste. Marguerite river when he noted the location of Otelne in his time (1861) as being on Aswanipi (Ashwanipi) Lake.³³ Change of residence of later hunters of the Otelne lineage may be imagined to account for this through marriage and matrilineal shift. He also mentions another, Akaske ("Arrow," *akask*), whose name, however, was not so far as we know, transmitted as a surname in any of the regional bands.

SMALL HUNTERS

A categorical classification prevails in the ranks of the Indians who make their summer rendezvous at the Seven Islands post, between the great "illustrious" men who lead their lives in the far remote plateau and those of lesser fortitude and station who hunt and trap on the lower course of the Ste. Marguerite and Moisie rivers and tributaries. Among the traders the first ranking is designated the "big hunters", the second the "little hunters", or irregular men, since they frequently change their hunting districts by common arrangement. In this verbal distinction—there being nothing official in its application—we may recognize what has long been understood among the Indians themselves as constituting the divisions of the *notcimi'wilnu'ts*, "interior or remote forest people" (also known as *pi't*, "inside") and the *winipe'gwilnu'ts*, "salt-water, or coast, people." The latter are, moreover, now to a large extent mixed with French blood and assimilated in habits and properties with the Canadian *habitants*. Hence the lower esteem in which they are held. In the list to follow is given the series of those families so classified by informants at the post.

It is patently evident that the stage of the "little hunters" represents a later phase in the history of society and economy among the bands of the region considered here. This example of change with sequence should, however, be handled with caution in any overt attempt to apply it as a broadside for interpretation of his-

³³ Hind, *op. cit.*, Vol. 1, p. 248.

torical conditions among other bands. The hunting territory institution may as well have developed into the communal band type of economy as out of it if we take single instances of one or the other as the definite case for the whole area of Montagnais-Naskapi occupation.

8. Johnny Pilo, a mixed blood, about whose family composition information is lacking, has locations west of Ste. Marguerite River, about 80 to 100 miles north of Seven Islands. His family derivation was given as of the Moisie Band where others of the surname are listed. Whether however, his privilege is accounted for by marriage with Ste. Marguerite Indians, or by assignment through tribal or post authority was not ascertained. The tract he operates, as given, is from Rivière Vallée north about 35 miles to R. Gamache, and 25 to 40 miles back from Ste. Marguerite river.

9. Charles Jourdain, 75 years old, now retired from active hunting and trapping, had four sons and one daughter. Three sons are now living and hunt upon the same paternally inherited territory which old Charles Jourdain says his father and grandfather used before him. This provides another case of three or four generation occupancy of the same territory and continuance in the paternal line with patrilocal residence of married couples. The three sons, filial partners, are Teddy, Alexandre and Antoine. Antoine has recently married the daughter of his father's brother, an example of parallel-cousin mating. For this "privilege" he is obliged to pay a penalty to the priest at Seven Islands out of his next year's fur catch. The Jourdain territory lies east of Ste. Marguerite River northward from about Grande Portage and Lac au Poëlon to about R. Athanase, a stretch of about 25 miles, between Ste. Marguerite River and the northwest branch of Moisie River.

10. Joseph Vachon, nicknamed *Wacaucoje'p*, "Bay Joseph," works a territory adjoining the mouth of Ste. Marguerite from Seven Islands bay westward, and just back of the coast, to where the Shelter Bay families come down. His adjacency to the bay has earned the sobriquet. The tract is hardly more than 25 miles in breadth and is unproductive except for small game.

Vachon has held the nominal office of Chief of the Indians congregating at the Seven Islands post from a period dating around 1915 down to the time when these investigations were made (1925). He is consequently the official representative of the Ste. Marguerite and Moisie

bands in matters relating to the Province. His authority is, however, insignificant, and is not recognized by Sylvestre Mackenzie, the head man of the families who come down from the remote plateau, *i.e.*, from Michikamau.

11. George Fontaine, a young man with several immature children, ascends the Ste. Marguerite to a location on its west bank north of the territory of Johnny Pilo, and works the country westward some 25 miles, stopping where Rivière à la Bataille comes in to mark his district from that of Alexandre Chelnish. Fontaine is a mixed blood who divides his efforts between trapping and working when opportunity comes at the Seven Islands post.

12. Joseph Oshogan (*oco'gan*, "hip bone"), concerning whose family composition no data were obtained, operated a district between the Ste. Marguerite and the northwest branch of Moisie river, 10 to 20 miles in depth, from about Rivière Athanase to near R. aux Pins, some 25 miles.

13. Joseph Fontaine, who bears the nickname *Mui'yak*, "Eider duck," and, as our data indicate, his brother François Fontaine (*Wucapi'pi*, "gall"), have a location on the east and west sides of Ste. Marguerite beginning a little below R. Dumais and R. Vallée, and extending north about to Lac au Poëlon. The Fontaines are small hunters and operate a small tract of some 15 miles of non-productive country largely depleted of its animal life. We have little to offer regarding their family which rates as French mixed-bloods.

It is worth noting in respect to preferred custom that the Ste. Marguerite hunters agreed, when the matter was opened for general discussion among them after the separate men and their families had been questioned, that some habitual principles were held to in the division of hunting and trapping land. The father of a family who has sons coming into activity will let the boys hunt one section while he does another. They plan to meet together only about once a month, during the course of the winter. Their working stock comprises between 200 and 300 traps. Exceptions are admitted in the arrangement when occasions arise to make readjustment expedient in the family economy. The meat and fur supply is not secured by the use of rifles to as great an extent as might be thought, for it happens that the Ste. Marguerite hunters in 1924 ordered only six new rifles for the following year's business. They now use 303 Ross-Lee-

Enfields, having changed from Winchester 40-4 for which they do not now care. Muzzle loaders are, however, kept in the winter camps as reserve weapons in case of emergency resulting from breakage of the more complicated machinery of the modern pieces which they are unable to repair.

FELONY ON THE HUNTING GROUNDS

A fair picture of the conduct of the Ste. Marguerite hunters could not be drawn without referring to statements made by certain of them concerning the unethical tendencies of members of the Fontaine families to "pull traps," *i.e.* to remove the contents of others' sets and possess themselves surreptitiously of the pelts within reach. A similar complaint was registered for some of the Jourdain family, though to a lesser degree. There was no hesitation among those who made these disclosures in mentioning such facts. Otherwise the irregularities cited were stated to be practically unknown in the conduct of the combined bands throughout the zone of their operations. The proper procedure for hunters in passing through the territory of others is to skin any animal found in the traps of the local proprietor and carry it until a time when they meet and it can be given to the owner of the traps and the trap line. An instance of the kind—reprehensible in the eyes of the men—was cited during the past winter when Alphonse St. Onge of the Ste. Marguerite group passed through the land of Joseph Mackenzie of the Moisie band, and found two martens there which he brought down to the post and sold.

It is most important in this connection to have a statement from the men themselves pertaining to their own beliefs as to what is the factor in restraint upon the petty larcenies of which they accuse certain of their band comrades, particularly in view of the circumstance that no violence is on record as a result of such misdemeanor. Neither is there reference in the discussions invited from their lips, to action by the so-called superior authority of the "chief." The only answer evoked from various sources was the explanation, given in the manner of a bated obvious result, that a spell of bad luck would ensue. The quality of fear is present and trespass has become imbued with a feeling of lurking menace from conjurational sources if not the supernatural resentment of the animals themselves to cause vague misfortune, sickness, game depletion, accident, or some other of the nameless dreads

menacing their existence without let, to add to the trials of life. Approach to the question was much the same in response; nobody wished to be explicit as to the form of spiritual persecution that might follow. They seemed to understand this vagueness and expected Speck as well as others of a questioning mind to do so. Equally important was the conclusion that no retaliation either social or physical was ever enacted. No one, for instance, presumed that a hunter whose traps had been lifted would perpetrate a similar act of stealth upon his offenders. A generalized fear of a spiritual avalanche of bad fortune settled the repeated attempts to sound the reasons for ethical self-control in the matters of property rights in the forest domains.

The remarks just made apply to all the bands dealt with in this report. It might be interesting to add that in the vernacular of the traders who are most familiar with aberrations of this type, and who, indeed, occasionally see fit to rectify them over the counter, designate the prohibiting force as the fear of "hoodoo."

The evidence we have here of a protective force, spiritualistic in character, carrying a menace of retribution hovering over the family food-producing districts, is significant of deeper implications in regard to the history of land-tenure beliefs. It conveys a sense of basic originality, it would seem, for the land institution with which the religious concept dovetails. Could we discern more instances of practices fitting into the religious system of belief, a clearer idea of their age-place might be forthcoming. It will mean something in the understanding of the history of hunting territory institutions if a more extensive series of practices accumulate in our records to ground them in religious thought which we are accustomed to associate with antiquity.

In addition to the heads of families previously listed as big and little hunters, there are some half- and quarter-bloods who hunt irregularly over the country near the coast wherever they can find fur and flesh from season to season without being recognized as having preempted rights or any other form of claim to holdings. From the point of view of the interior hunters, they constitute a proletarian class and are considered more as Whites than Indians. Their occupations are varied; small hunting, trapping, intermittent labor for the Canadians of the coast, and guiding sportsmen in the hunting and fishing seasons. They are derived from the older families through second and third, or more,

generation mixture with the French *habitants*, having for the most part French surnames. And they reside permanently in houses in the village of Seven Islands in a quarter at the north end of the single long lane, following the shore of the bay, which forms the main street of the settlement. Batiste Picard, *Nabeoco'*, "Old Man," is one of the type who resides at the post, does odd jobs thereabout, interprets, mends canoes and on occasion makes a small trapping excursion into the bush to relieve matters. His sons hire out to explorers, sportsmen and to other Indians who need help in their territories and pay on shares. His brother Ange Picard, however, casually operates a small and depleted district on the lower Moisie (Moisie, No. 1) and consequently is listed with the Moisie band.

SHELTER BAY BAND

In 1925 the status of the several family groups comprising the Shelter Bay Band was very difficult to settle in regard to relationships and earlier history. The individuals comprising the band were almost completely merged with the general population of the combined offspring of the earlier more distinct divisions that now assemble annually at Seven Islands. The Shelter Bay individuals are all much mixed with French blood. Three families represent them:

- a. Tcibās St. Onge
- b. Francis St. Onge
- c. Malekis Vollant

That something of a separate identity has either remained from a former grouping or been developed since the days of intense trapping and trading with the Hudson's Bay Company and with the infiltration of alien blood may be shown in the name *Wesakwopata* (*a'n wi'lnut'*, "People of the Portage," which has come to be locally assigned to them by other Indians. This name is derived from that of the river *Wasa'kwopata'gan cib'u'*, interpreted as "Mossy Portage River", upon the waters of which they travel and hunt inland for about 100 miles. The St. Onge family claimed to have occupied this tract since the time at least of the grandfather of Tcibās, who was approaching seventy years of age. Tcibās St. Onge was the father of Francis. The latter was married, had a large family of children, and resided on the waters of the same river, having received a partition of the paternal district. The father of Tcibās St. Onge was Dominique St. Onge whose age at the time of his death was above ninety. This man had the distinction of

being mentioned by H. Y. Hind, previously referred to. Hind had considerable to do with the then young Dominique who, when Speck met him in 1913 was still active despite his age and living with his wife. He told Speck that he had had eleven sons of whom two only were living. His father, he asserted, was a Micmac from Gaspé, who had located on the north shore of the St. Lawrence and married a Montagnais-Naskapi woman, hunting the same territory that he had. There is, in consequence, some uncertainty as to the original content of this small band. It is probable that the mother of Dominique, the oldest of whom we have definite knowledge, may have been the inheritor of the Shelter Bay region which has since passed down through the male line to its 1925 holders. The other family head of the band, Malekis Vollant, was married to one of the St. Onge women, so here we have a case of matrilocal affiliation. The Vollant family, as noted, is properly attached to the Moisie Band. The Shelter Bay hunters on account of their nearness to the Seven Islands rendezvous spend much time at the post. They leave in November, come out from their hunting grounds once during the winter, arriving about January first, and leave again in February to stay in the bush until March. The distance from salt water is about 60 miles. There seems little more to note concerning the history and habits of this small band. It has no distinctive traits, and is evidently to be considered as one of rather recent foundation.

It should be noted, perhaps, that Speck found testimony to show that Tcibās St. Onge and Malekis Vollant have moved from former hunting grounds on the lower Ste. Marguerite river to their present locations on Shelter Bay river. The statement is evidently more applicable to Malekis Vollant, since we know that his father (Malek V.) was affiliated with the people in the neighborhood of Seven Islands bay, and that they now are members of the same line in the Moisie Band. The three hunters and their wives, a brother of Francis, the five children of Francis, and one son and two daughters of Malekis, made a total of some fifteen members of this gathering. Three of the hunters had adopted patrilocal residence and two of them matrilocal residence at the time of inquiry (1925).

NICHIKUN BAND

The Nichikun band has been dissolved as a social unit since the abandonment of the Hudson

Bay's Company at Lake Nichikun circa 1919. The band is indeed an old one, being indicated upon charts of the 17th century in the same location that we find it now. Some particulars were given in the article in the *American Anthropologist* referred to already.³⁴

Members of this band were met with during several periods when Speck was working at Seven Islands in 1915 and 1925. Following the dispersion of the families of the band, he was told that some took up their residence with the Moisie Indians while others joined the bands west of them. The only mention of the Nichikun band that bears the mark of definite attention upon specific circumstances of this band is that of A. P. Low (1895), which is as follows:³⁵

"These Indians belong to the western Nascaup-pee tribe. They speak a dialect closely resembling that of the Montagnais. The men are of medium height and fairly good physique. Some are tall and well developed, but the average height does not exceed five feet seven inches. Like other Indians they are sinewy rather than muscular. As a rule they are less cleanly than the Montagnais, taking little care of their clothes or persons; and they generally swarm with vermin. Owing to the small numbers of caribou killed in this region, the natives are forced to clothe themselves in garments bought from the Hudson's Bay Company. They live in wigwams covered with cotton, as they cannot get either the deer skin used in the north or the birch bark covering of the south."

"The hunting grounds of the Indians of Nichikun extend from the Height of Land on the southward, to the headwaters of the Great Whale River on the north. To the eastward they hunt as far as Lake Kaniapiskau and down its discharge about fifty miles. . . . The greatest number hunt to the westward of Nichikun, or about the headwaters and tributaries of the Big and East Main rivers."

"During the summer they subsist almost wholly on fish caught in nets in the lake. . . . During the winter the living is better for then . . . they are able to obtain . . . fresh meat. About a dozen caribou are killed by the people of the post during the year, besides beavers, muskrats and bears. Usually rabbits and ptar-

migan are abundant during the winter season and are shot and snared as required. In some years, however, both rabbits and ptarmigan are not plentiful, and caribou are scarce. During such seasons the food supply is very limited, and great care must be taken to avoid starvation. . . .

"There are about thirteen families of Indians who trade at this post, but this does not represent all the people inhabiting this portion of the interior, as a number of families prefer to descend to Rupert House and trade there. . . . Others living to the southward who formerly traded at Nichikun, now descend the rivers flowing into the Gulf of St. Lawrence."

Hind in referring to the natives who frequented the region about Pletipi Lake, which he says was three days' journey from Lake Mouchualagan inhabited by Montagnais, designates them as Naskapi.³⁶ It might seem from this that his informants regarded them as associated with the Nichikun who are nearest to them. Until, however, the composition of the populations making their rendezvous at the Bersimis post has been worked out this point will be left open. At the time when these records were made the men of the Nichikun band encountered at Seven Islands were so recently thrown into the newer associations of an alien adjustment that it was difficult to arrive at a clear understanding of the past and present grounds where they worked. They also seemed suspicious.

The list of families of the band at the time of their dispersion is as follows, given me by Joseph and Peter Hester, at Seven Islands:

Tcwa'li	(one daughter, two sons)
(This man was chief, holding his authority for life. His father was chief before him.)	
Joseph Hester ³⁷	(two sons, one daughter)
(Peter Hester, Kokuc ("Pig"))	
(Débid (David) Hester, Wapatci' ("Tomorrow Morning"))	
(three sons, two daughters) brothers	
Alphonse St. Onge ³⁸	(no children)

³⁶ Hind, Vol. 1, pp. 197-200.

³⁷ Peter and Debid (David) Hester are the sons of old Joseph Hester who came originally from the Rupert House band. Joseph Hester had previously hunted with his father-in-law, Dominique, *Ntagwonic*, "little medicine." He did not have much success over a period of four years with his affinal father-in-law. Then he returned to his paternally inherited tract in the year 1924. This individual case well illustrates the adventitious character of the hunting arrangement, determined by environmental circumstance rather than an exacting social pattern of behavior.

³⁸ Alphonse St. Onge (40 years old) son of old Tcibās

³⁴ Speck, *op. cit.*, p. 591.

³⁵ Low, A. P., "Report on Explorations in the Labrador Peninsula Along the East Main, Koksoak, Hamilton, Manicouagan and Portions of Other Rivers," *Geological Survey of Canada*, Ottawa, 1896, pp. 100-101.

Pieni'c ("Little Pierre")	(no children)
Pilipi's ("Little Philip")	(four children)
Nte'bit'	(four children)
William Tcali (son of Tcwali, above)	(four children)
Ayi'cuk'w (meaning ?)	(no children)

Assuming that the wives of the family heads, listed above, were living, the band would total around 40.

Questioning disclosed the fact that the Nichikun families did not separate and hunt or trap alone on inherited hunting grounds, as do the Montagnais south of them. So far as conditions of the game and season will permit they all hunt together.

Speck was informed by the Hester men that before changing the trading route to the Seven Islands Post, they descended to the Rupert House in six-span canvas canoes. The change at the time of this visit (1910) had effected some striking results in their condition. The hunters listed had married or intermarried with French-speaking Indians trading at Seven Islands, had come under the sway of priests where they had hitherto been adherents of the Church of England and, in addition to their English were using Canadian French with no less fluency than the Seven Island natives.

MICHIKAMAU BAND

The group now to be considered derives its name from Lake Michikamau and so bears the designation *Micikamo'i'nuts*, "Great Lake People." The area of land usage traditionally preempted by its members in support of life centers around this immense body of water which lies considerably north of the Height of Land.

The Michikamau horde is apparently the most integrated of the groups living in the central interior of the peninsula. The isolation of their habitat and the recency of their emergence from solitude into the confusing *milieu* of life at the Hudson's Bay Company's post at Seven Islands have tended to preserve their social independence

St. Onge, has no children of his own so he has adopted his brother's widow's son, now four years old, to bring up as a future helper. He winters and hunts a territory about 60 miles in diameter around Lake Attikopi Lake, which lies north of Nichikun, and also Eagle river and lake. His route begins about a day's journey by canoe from the former Nichikun Post. This man evidently represents a later distribution of hunters after the dissolving of the Nichikun band proper, since he is of a younger generation than Tcibās who is a procreator of the Shelter Bay Band.

and to fend off the disintegration through mixed marriages and adoption of French-Canadian ideals and manners. Sickness introduced by contact with the coastal populations has also begun to have its effects. The cohesion of the band depending largely upon caribou for food is nevertheless noticeable by contrast with others who hunt in segregated family fashion over a larger part of the year. The authority of its chief, Sylvestre Mackenzie, a leader by nature of his personality, authoritative and practical-minded, is pronounced, and may be a contributing factor to the unification of the horde. The salient data pertaining to this band, given in the report of 1931, from which summaries have been quoted for other bands, may be cited here:²⁹

"The environs of Lake Michikamau, chiefly between this lake and Petisikapau, about 100 miles in extent, are embraced within the limits claimed by the hunters who give this name to their group.

"The band has not apparently attracted the attention of previous travelers or writers. Therefore it is upon the testimony of its chief, Sylvestre Mackenzie, and other members that I base my assumption of its existence as a band unit.

"The Michikamau Indians live and hunt almost continually as a community of grouped families. Only when pressed by famine do they separate and live upon small game. At other times it is the caribou that supports them. Under the jurisdiction of the chief, the group comprises thirteen family heads who are practically all related by blood and marriage.

"Until recent years this band went to Northwest River for trading purposes. Now its members in one large company make the long and dangerous descent from their distant lake to the post at Seven Islands by way of Menihék Lake, Ashwanipi Lake, and Moisie River each year."

The migrational cycle of this band to and from its interior domain to the coast at Seven Islands is interesting from the light it sheds on the matter of time and energy spent annually by the human drove in the peregrinations of trade. The chief, Sylvestre Mackenzie, gave Speck the outlines of his travel narrative in 1924. Punctually on August 1st the band leaves "salt water" (Seven Islands) ascending Moisie River, passing through Kaopasho Lake and then across the Height of Land, reaching Menihék Lake by about October

²⁹ Speck, *op. cit.*, pp. 589-590.

5th. Here they camp to fish and hunt for a few days. Thence they move along by easy stages to Michikamau, hunting and fishing and reaching their destination at Michikamau by the end of October. From here they plan to separate into family groups for a season of trapping to accumulate fur. It is essential before this temporary dispersion that they decide upon the place where they are to gather—the first rendezvous of the winter. Sometime in November this takes place. From this time until toward the end of January they travel as a band, depending upon and following the caribou for food. This is the mid-winter hunt. Around the end of January, the great period of casualties should the caribou fail them, they separate again by families to pursue trapping in their habitually frequented tracts. About the end of March or the commencement of April the entire "gang" (a traders' term) comes together again at the customary rendezvous on Menihek Lake. Here an extensive encampment of tented families soon congregates as it has for many generations—incidentally a promising place for stratigraphic archaeological work when opportunity is afforded. From then until the commencement of May the convening of hunters and their families goes on and the horde prepares to descend to the coast with the harvest of fur. Early in May the flotilla gets under way moving southward over the Height of Land, through Ashwanipi Lake and down the Moisie River, arriving at the Moisie post almost punctually on the 25th of June. This completes the cycle of the annual migration from interior to coast. It should be noted that some families as well as individuals, who for various reasons are unable to undertake the trek, remain at the Menihek gathering place over the summer until the return trip of the southbound flotilla is due the first week of October. They subsist chiefly upon fish. A few, we are told, may refrain from the coast migration for many years, some never going down.

It is a matter of judgment to what extent we may conclude that the insistence of fur traders upon increase in the production of skins by the natives had the effect of adding an incentive to the economy of the Indians, obliging them to divide their time on the hunting grounds between hunting for food and trapping for pelts. The division of labor between the two activities as just outlined would seem to be an adjustment to the demands of trade, with pressure from without exerting a stimulus upon trapping as a competi-

tive pursuit with food hunting. Assuming then that the food quest is an inevitable aboriginal occupation and that fur trapping has been accentuated since contact with Europeans, a chronological sequence may be postulated in the case before us. The economic pattern, either communal hunting in a horde or segregated family hunting throughout the entire winter or only part of it, can as well be conceived to fit the character of country and game by one system of pursuit as the other. The trapping activity, however, practically necessitates the separate family distribution of population over a wider area, and intensively in spots where fur-bearing animals abound. The magnitude of the recent change in the economic set-up of the Michikamau Indians is manifest in the fact that they now engage in the more arduous and consuming annual voyage from their hunting grounds to the Seven Island post than the trek to Northwest River as formerly. This procedure is in the endeavor to gain the advantages of better trade at greater expense of time and effort. Trade has become a moving impulse in their life calling. We may accordingly postulate the direction of change in the case of this band by placing the communal caribou hunting activity before the era of trapping in split-up family groups. But to apply the same gauge to every band in the Montagnais-Naskapi complex to prove the postulate would be to cheapen the methods of research by shape-shifting to a degree beyond the bounds of patience. To propose an explanation for economic change over a wide area of the north by assuming that the history of any one band is a recapitulation of the whole would be unjustified. In the theoretical discussion in our conclusion this fact must be carefully borne in mind.

A phase of the habit of preëempting precincts needed or necessary in the course of their hunting, trapping and traveling reappears in the social actions of the hunters who come out from the interior down to the coast at the Seven Islands post as a usage-right once assumed then transmitted by traditional agreement is yet to be noted. The flotillas of hunters and their families in canoes arriving in late June continue to use the same sections of beach year after year as landing places. Each band beaching and unloading and later loading for departure customarily appropriates a certain stretch of the short line for its own use. And the family components have theirs. No formality, how-

ever, governs the action. Interference does not occur. It is possible to determine from a distance the identity of a family by the station it makes upon its arrival and beaching. The members of the Michikamau band for instance beach and camp at the north end of the sweep of sandy shore beyond the Hudson's Bay post lot. The Ste. Marguerite hunters make their stations nearer the company's grounds.

In the periods of the winter devoted to the business of trapping when the family units of immediate relatives—the small families specifically—break up to resort to the trapping grounds for limited seasons of isolated residence, they distribute themselves habitually in districts preëmpted by long-maintained use. Sylvestre Mackenzie, chief, indicated the principal hunters of his "tribe" and the whereabouts of their customary fur harvesting during the seasons of band disintegration just noted. Corroboration of the locations recorded were given by the men of the band who witnessed the task. The plotting was, however, a somewhat confusing procedure in view of the serious obstacles to be surmounted in identifying and in tracing grounds by well-known names of lakes and rivers which were not shown upon any of the maps obtained for the purpose from the Dominion Geological Survey. The results accordingly are offered with these imperfections well in mind. Mackenzie also stated that locations were made by the hunters subject to his chiefly approval and with general assent by the others having in mind the welfare of the whole horde during the hardest part of the winter. Several of the hunters voluntarily drew sketch maps in pencil of their trapping grounds with the situation of their temporary seasonal camps marked out and the nature of the fur indicated. These are reproduced in figures 1 and 2.

Recorded through the channels of information just mentioned, the family heads and the data pertaining to them appear as follows:

Nabes Gregweneesh, *Wa'icakutec*, "Little woodchuck," a young man married to a daughter of Sylvestre Mackenzie resides with Sylvestre and follows him in his hunting and trapping movements. He marked off his area of operation as lying between Menihék and Dyke lakes when the season of separation for trapping comes. How to assign these hunters to bands is a question. The merging of the socially dissolved Petisikapau band with the families of the Michikamau area under Sylvestre Mackenzie is

instanced in the case above where matrilineal residence has taken one of the Gregoire men directly into the Mackenzie family group.

Pien Andre, (26 years old) who bears the sobriquet *Mict Ben*, "Big Ben," traps over an area south of Michikamau Lake toward Attikonak Lake as well as to the southeast of Michikamau. This man prepared a sketch map of the district and movements within it which he and his companions worked the winter of 1924-5. It is reproduced in Fig. 1. One of the observations recorded of him is that he sets 25 marten traps a day on his route. This he regarded as his major harvest in fur.

Openauk, "Black man," traps, whose name is derived from the extreme darkness of skin characteristic of the family.

Bernard Gregoire, son of old Bernard Gregoire who died in 1924, now traps in company with his mother.

Bastien Dominique and one son trap.

David Dominique also traps.

Mathieu *Kabec* and Gabriel *Nisipi'c* trap as partners northeast of Dyke lake.

Domenique Doctor and adult son constitute a two family partnership.

William Atela'o, also *Milwa'tem*, "Likes it." Joseph Germain.

Pierre Germain, *Menoka'bo*, "Stands firmly," and son who is married, make a two family group.

Gregoire *Potciga't*, "crooked leg," brother of the Gregoire family men who move with the Ste. Marguerite hunters.

Peta'banu, "Brings the dawn."

Joseph Mackenzie, *Wabiya'n to'gi*, "Rabbit ears" so nicknamed from the peculiarity of his ears. Brother to Alexandre and Sylvestre Mackenzie.

Alexandre Mackenzie and son (For illustration of his hunting districts see Fig. 2).

Sylvestre Mackenzie (chief since 1922). Brother to Joseph and Alexandre Mackenzie.

Mathieu *Djokabesh* (*djo'kabec*, the proper name of the Montagnais-Naskapi hero-trickster of mythology, but a name not satisfactorily translated) who is married to the sister of Sylvestre Mackenzie, together with Gabriel Nisipish of a similar relationship, form a trapping partnership, and operate in the spacious area of barrens north of Michikamau Lake and toward Dyke Lake. This group of families usually moves together in ascending and descending from the interior to the coast. It was stated that they hold feasts and

CHART SHOWING POSSIBLE MODES OF DEVELOPMENT OF BOTH BAND AND FAMILY TYPES OF OWNERSHIP OF HUNTING TERRITORIES AMONG THE ALGONKIAN OF THE NORTHEAST

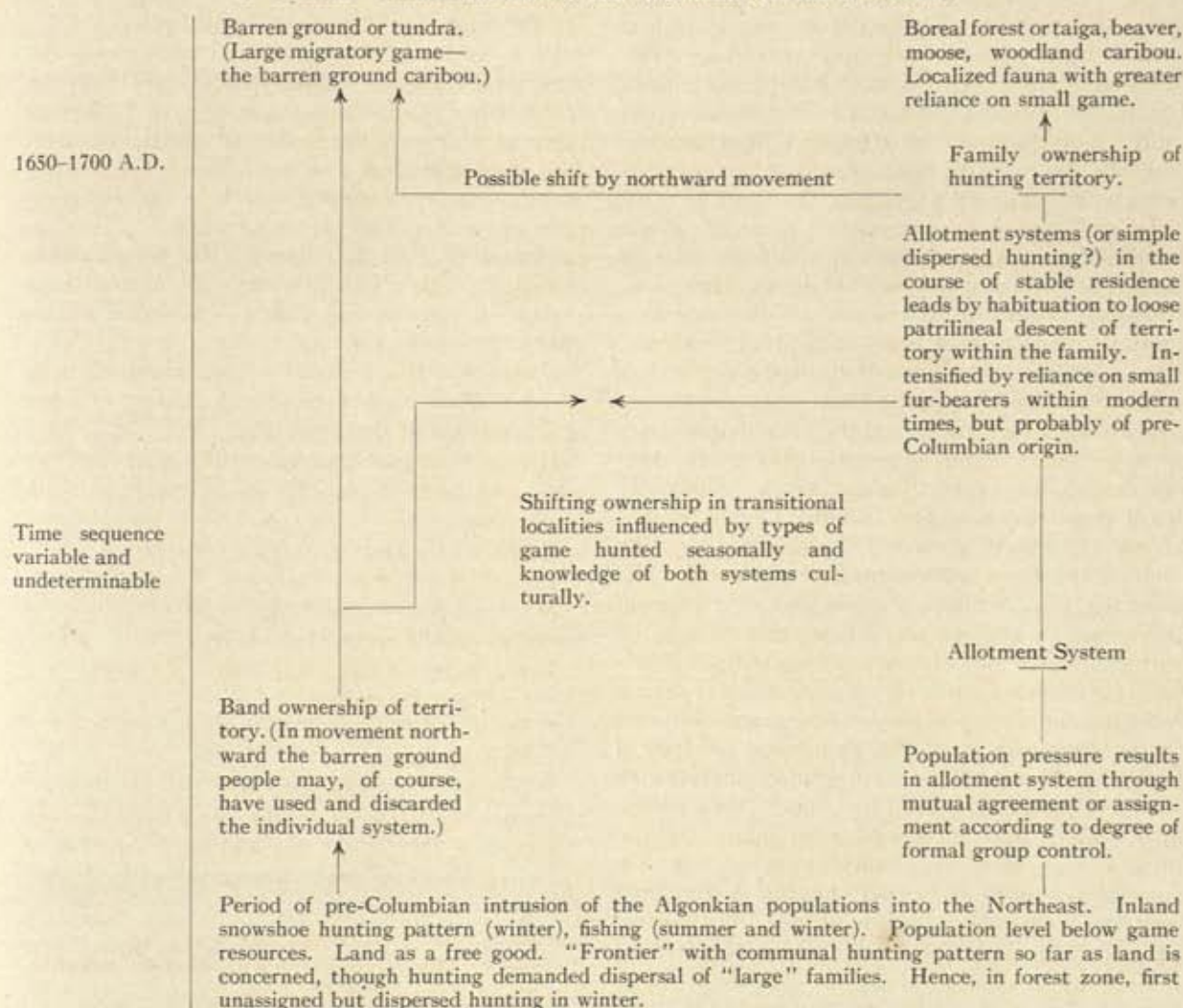


Chart showing distribution of Montagnais-Naskapi Bands of the Lower St. Lawrence and Labrador peninsula, with approximate location of family hunting and trapping districts (1922-25). (Drawn by F. Staniford Speck.)

dances at the times when they depart and arrive at their destinations en route.

John Pierre, or *Wa'pactan Piel* (*wa'pactan*, "marten") avowed himself to have been born in the Ungava district, hence a member of the Ungava Band. He still hunts a territory far northward of the grounds frequented by those men previously noted. There were, at the time of contact with him, no feasible means of designating on the map the area he tried to describe. In consideration of the fact that he moves from his grounds down to the coast to trade, joining the migration cycle of the Michikamau hunters, it

was thought advisable to list his identity with the latter. This was done partly because of his submission during the treks to the authority of the Michikamau head man Sylvestre Mackenzie and his probable marriage connections there, but chiefly because of his interesting family makeup. *Wa'pactan Piel*, as he was commonly called, had no son but two daughters nearly of one age. These two women were "wives" at the same time of an active hunter, Ben Kabesh (*Kabe'e*, an alleged shortened form of the name *Djo'kabec* the proper name of the hero-trickster of mythology). It is probable that he is a member of the family

of this name which herds with the Michikamau group (see Mathieu Djokabec above). This instance not only illustrates marriage of the sororate pattern but matrilineal residence. By common repute Ben Kabesh married one of the daughters and went to live with his father-in-law in the same tent. It was not long before he had a child by each (of the "wives") in turn. He still dwells with Wápæctan as a partner in the chase. Marten trapping is a major pursuit with these men and is the source of origin for the sobriquet borne by Piel. This incidentally affords a view of the habit of acquiring personal name identity from the principal animal taken and killed by a hunter—personal "game-totemism" *ipse licet*.

It is evident from the information furnished by these men, fragmentary as it is, that the Michikamau band is a vital illustration of the basically communal hunting horde which under force of circumstances modifies its social procedure to the family type of residence during part of the winter. That the annual economic cycle is split into the several types of organization is the feature of importance here in our survey of hunting systems. It next remains to seek out the factors and influences which explain the variations observed and to piece out their historical sequence if possible by logical interpretation.

CONCLUSION

The conclusions which are derivable from the material we have just surveyed cannot, as yet, be grasped in their entirety. Too much needs still to be done in the field of circumboreal research before it will be possible to weigh to the full the influences, ecological in terms of game hunted, and cultural in terms of established tradition, which form the basis of property ownership among the lower hunters. Approached from the historical standpoint many questions arise. Does band ownership, for example, precede the family system? Does the assignment of land to individual families by the head man, as has been recorded in many instances, precede the direct handing down of territories within the family and is this latter method a purely historical development? Can a widespread succession be observed, or is local adjustment to local exigencies the only observable factor? These and many other questions present themselves for answer. Their shadow must inevitably be troubling to those who, like Morgan, and many

present-day Russians, would see the culture of the lower hunters as representing a stage prior to the development of the institution of individualized property. The solution is not easily given because, though ecological patterns seem to have been paramount in the production of the system we have just surveyed, anything which becomes traditional within a human group may be perpetuated, furthered, or modified beyond what might be immediately expected in the case of a new culture intruding into the same environmental background. It may be that this has played its part among the Athapascans who seem to lack the concept save where there exists a reasonable suspicion of Algonkian contact. Elsewhere, the writers have hinted at the functional reasons for the development of the family hunting territory system. Let us attempt a more detailed descent into this pre-Columbian world and see if out of environmental and cultural interplay unmodified by white contact, any evidence exists for sequential stages in the development of an institution which strikes the social theorist as such a curious cultural excrescence to be found among primitive nomadic hunters.

In the first place, it is reasonable to assume that in any new, unpopulated territory being penetrated by wandering hunters small in numbers and not, as yet, pressing heavily upon the game supply, land will tend to represent an economically free good. This will tend to be the case whether or not the requirements of hunting demand united or dispersed effort. It is what we might term the "pioneer" period before the pressure of population and long-term residence create greater territorial consciousness on the part of the group. Such conditions must undoubtedly have fore-run the more intensive ownership patterns now present among the Algonkian hunters, but at what point in their range the change was initiated, how many times duplicated independently or spread by contact, we cannot answer. We can, however, definitely perceive two separate ownership patterns which, as previously indicated, are adjusted to the type of fauna exploited: the band ownership of hunting territory which obtains among those who pursue the migratory caribou herds of the tundra, and the system of family hunting territories, either by mutually agreed seasonal allotment or loose patrilineal inheritance which exists among the hunters of the forest zone who must exploit, in family isolation, the more scattered woodland caribou, the beaver, and like fauna.

Returning, however, to our postulated stage of pioneer penetration and "free" land, it may be seen that as population grows, and, in addition, remains in the new area, increased band concern with the territory and its wild denizens will take place. The band will grow ever more conscious of its dependence on a particular area and food supply.⁴⁰ (What indeed were the hunting policies of the plains area but the exhibit of a similar concern under the pressure of a larger, more politically conscious population?) Intrusion of new peoples will be resented. This will be the obvious limit of land consciousness so long as the group is pursuing more or less migratory game, such as the barren ground caribou, in a manner which demands not individual, but group effort. All that has really developed is some added consciousness, perhaps, of group need to protect its area of group exploitation.⁴¹ This, of course, is the sort of situation which Morgan visualized as being omnipresent in the stage of savagery,⁴² and implying an entire lack of individual property concepts in land. Land ceases to become a free good as population reaches the survival limit upon it under a given form of economy. The whole history of our pioneer west, from the free range to the coming of the small farmer illustrates this same basic struggle in another guise. Free land is frontier land and, indeed, Speck has observed a tendency for the hunting territories to be more restricted in size where settlement has been longest maintained.⁴³ Along with their undoubted distinct

ecological adjustment the hunters of the subarctic are, in a sense, still pioneers where land is wide and population small. Thus may be postulated Stage I as a period of variable length and circumstance where land is practically valueless because the existing population is not capable of its full exploitation and there is plenty of choice allowable to both the single hunter and the group. This condition, in the case of the localized fauna, results at first in dispersed, but unassigned hunting activities.

Out of a certain degree of permanence of residence will then develop a sense of band territorial possession which, under ecological conditions leading to dispersion of effort in the hunt, may also trend in the direction of individual family exploitation of a given territory. This, it has been noted, may take the form of the allotment system either by the head man arbitrarily assigning territories for a season, or by mutual agreement among the hunters.⁴⁴ As we have noted previously this system may exist in conjunction with communal hunting and alternate with it among the same people in some instances.

It may be suspected that the allotment system by choice or assignment preceded the permanent family ownership system since at some point selection must have preceded continual occupation for a long enough period to set up traditional family occupation of one territory. The one, however, could easily pass into the other as

⁴⁰ Steward, Julian H., *Basin-Plateau Aboriginal Socio-Political Groups*, Bulletin 120, Bureau of American Ethnology, Smithsonian Institution, 1938, p. 254. "It may be postulated that habitual use of the resource in question by the family, village, band or other group was a necessary condition for the development of claims to it." This comment by Steward, for another area, clearly indicates the ubiquity of this working principle.

⁴¹ Hershkovits, M. J., *The Economic Life of Primitive Peoples*, Knopf, 1940, p. 292. "Full-fledged communism in land thus means that land has no economic value at all except in so far as the holdings of a given tribe are contrasted with the lands of another entire tribal group whose encroachment on the territory of the first tribe is to be resisted by force."

⁴² Morgan, Lewis H., *Ancient Society*, Charles Kerr & Co., Chicago, 1907 edition, p. 537. "Lands as yet hardly a subject of property, were owned by the tribes in common."

⁴³ Speck, F. G., "Basis of American Indian Ownership of Land," *Old Penn Weekly Review* of the University of Pennsylvania, Vol. 13 No. 16, 1915, p. 495. "Culture Problems in Northeastern North America," *Proceedings of the American Philosophical Society*, Vol. LXV, No. 4, 1926, p. 303.

⁴⁴ The allotment system through arbitrary assignment of territories by the headman is somewhat hazily presented in the literature. Dr. Cooper, for example, points to the weak and shifting character of the band and indicates that the so-called "chief" of the early writings may have been no more than the head of a large family splitting up the activities of his dependents upon his own territory by allotment, seasonal or otherwise. Unfortunately, particularly in the early writings, the band, in many cases, is not clearly distinguished from what may have been large land-owning families. In fact, as Steward has been led to suggest, in some cases large families may have eventually become patrilineal bands. The writers have elsewhere pointed out that allotment may also have been of more significance where the office of chief was invested with greater authority. We are inclined to concur with the opinion of Dr. Cooper that the allotment system is strongly in need of clarification and that a good deal of the early literature in particular is somewhat suspect on this point, though not as to the existence of the individual territories. See J. M. Cooper, "Is the Algonkian Family Hunting Ground System Pre-Columbian?" *American Anthropologist*, Vol. 41, 1939, pp. 71-72. Also Julian Steward's "The Economic and Social Basis of Primitive Bands" in *Essays in Anthropology Presented to A. L. Kroeber*, University of California Press, 1936, p. 339; and Speck and Eiseley, *op. cit.*, p. 277.

hunters raised on a particular territory could act more efficiently upon it. Families occupying a particular spot for any length of time would be bound by habit to utilize the territories each knew best and hence patrilineal descent of the loose flexible type which has been noted could be introduced almost imperceptibly. That in modern times true family ownership has been stimulated by the intensive exploitation of the fur-bearing animals may be admitted. Nevertheless, the weighty evidence for pre-Columbian game husbanding of such animals as the beaver is a potent argument for the existence of family territories of something more than a seasonal variety.⁴⁵ Why else would such care be taken of this non-migratory beast? Certainly the allotment hunter, unless his allotment were of a pretty permanent nature, would be less interested in restraining his cupidity. In fact Schmidt has argued that one incentive for the establishment of the family territory system lay in the fact that it made for better regulation and husbanding of the game resources and was more easily handled by the head of a family in relation to his children.⁴⁶ Indeed he goes so far as to suggest that perhaps the so-called assigning of land by the chief may, in some instances at least, have been no more than the adjustment of inheritance claims.⁴⁷

Where, as in the higher arctic, human population is reduced to such a degree that the individual is forced to move over very wide areas or rely heavily upon the sea, property concepts in land are dimmed even though the life struggle is intense. But below, in the forest zone, where the brooks of a particular watershed may support a localized fauna which with husbanding may support a family in some faint degree of security, the aboriginal will grasp the desirability of outright possession more quickly because human competition in the life struggle is more readily apparent. And with every generation that a particular family holds such a tract where the supply is limited the more firm is the ownership pattern likely to become.⁴⁸ It must inevitably

confront the careful student of the problems which we have been considering that in the search for the origin of the Algonkian family hunting territory system four approaches are possible. First, the already much discussed historical explanation, linking it with the fur trade—an explanation criticized elsewhere.⁴⁹ Second, an explanation entirely in terms of the ecological background. Third, as a survival, culturally, of an archaic Algonkian trait of which the origins are thus merely extended into a more nebulous past. Fourth, an explanation which would emphasize the ecological approach but leave room for the acceptance of possible cultural factors which may have extended or retarded the diffusion of the trait.

Dr. Cooper in his recent excellent survey of the hunting territory system⁵⁰ takes some note of ecological factors at work in producing the institution, but, without entering fully into this phase of the discussion, he points out the presence of somewhat similar developments in South America in a few instances, and seems to hint, at least tentatively, at the possibility of the pattern being an archaic survival in the New World. Also he brings forward a genuinely puzzling point—the apparent lack of a similar system among the northern Athapascans even though the beaver range is circumboreal.⁵¹ This is admittedly a difficult problem, in part, we would emphasize, because so little is known in detail of the eastern Athapaskan territory. Are we justified, for example, in assuming that conditions are entirely the same?

Dr. Steward after an intensive survey of band conditions in all parts of the world has expressed himself as being of the opinion that only rarely would individual land holdings on the hunting level of society be sufficient to sustain life, after the exceptional Algonkian pattern. In this connection, though recognizing our dearth of source

⁴⁵ See Speck and Eiseley, *op. cit.*, i. n. 11, p. 273.

⁴⁶ Schmidt, W., *Das Eigentum auf den ältesten Stufen der Menschheit*, Münster, 1937, Band I, p. 152.

⁴⁷ *Ibid.*, p. 154.

⁴⁸ Herskovits, *op. cit.*, p. 293. "The emotional attachment of men to the districts where they were born and to the particular localities over which they have exercised proprietary rights, as well as magical and religious considerations, are powerful non-economic forces which must be taken into account."

⁴⁹ Probably the most extended defense for the historical origin of the hunting territory system among the Algonkians is to be found in a work by Alfred G. Bailey, entitled *The Conflict of European and Eastern Algonkian Cultures*, New Brunswick Museum, monographic series No. 2, St. John, New Brunswick, 1937. It is interesting in connection with our previous emphasis upon the significance of beaver hunting that Bailey himself (p. 9) admits that the Indians "prize beaver above other animals" not only as food but for clothing, and this before the fur trade had been intensively developed.

⁵⁰ Cooper, J. M., "Is the Algonkian Family Hunting Ground System Pre-Columbian?" *American Anthropologist*, Vol. 41, 1939, pp. 66-90.

⁵¹ *Ibid.*, p. 81.

material, the writers would call particular attention to the following facts derived from Dr. Steward's previously mentioned article.⁵² He points out in a cursory survey of the Athapaskan area that, in contrast to a population among the Algonkians ranging from one person per 5.3 square miles north of the Great Lakes to one person per 34.6 square miles in the eastern subarctic, the Athapascans average one person per 50 to 80 square miles with "some regions being virtually uninhabited."

We quote further: "The bands of the eastern or mainly Mackenzie Basin Athapascans are extraordinarily large in view of the sparse population, numbering several hundred persons each. This surprising size must be explained by the local economy. There are large herds of migratory musk ox and often caribou in much of the area. These are hunted more or less seasonally and collectively by large groups of people."

The facts just noted suggest a severity of life among the Athapascans not quite comparable to that region in which the hunting territory system achieves its clearest development. Instead we encounter greater reliance upon migratory game and the presence of that constant "frontier" of which we have spoken, where the coöperation of groups moving over wide areas in the struggle for life dims out familial localization and competitiveness. The trap-line ownership coming in in this area is a late development on the part of a people inclined more heavily toward the pursuit of migratory game and only taking up with individualized hunting in a serious manner as the beaver and other small fur-bearers assume more importance economically.⁵³

We do not feel that sporadic cultural developments of a similar nature in other portions of the world need necessarily be linked with the Algonkian system as survivals of ancient waves of diffusion. It is not likely, in any case, that

⁵² Steward, J. H., "The Economic and Social Basis of Primitive Bands," *Essays in Anthropology Presented to A. L. Kroeber*, University of California Press, 1936, pp. 339-340.

⁵³ The actual numbers of beaver in various parts of its range are not well known. Its vision is by some writers reputed poor and it needs an abundance of water to best protect itself from wild carnivores such as the lynx and wolverine. Hence to say that it is circumboreal in distribution is not to indicate its exact numerical or ecological importance to man in all parts of its range. Where bigger game was more significant the beaver even when present may not have been, culturally, of so much importance. A systematic, localized and detailed study of faunal-human relationships in the north has still to be made.

so fluid a concept would long survive unless based on group necessity. Certainly its loss among the arctic Algonkian hunters or their casual swing from one practice to another does not encourage its treatment as a static element of culture. Instead we view it as the response to conditions in a forest region not too productive in terms of large game, but having a small fauna (primarily beaver) which could be husbanded and manipulated rather successfully by individual families, whereas a large group might starve on the same territory.⁵⁴ Somewhere in the forests south of the barrens or tundra area the pattern began. It is known historically both north and south of the St. Lawrence. Whether apparently similar though less clearly elucidated practices in aboriginal Siberia represent similar adjustment or instead a cultural survival related to Algonkian practice is a difficult problem.

The ecological background conducive to the family exploitation of game resources grows, as we have indicated, out of conditions of family isolation which in turn are caused by the necessity of deriving sustenance from a not too rich, not too easily securable but definitely localized fauna which cannot be hunted communally. Against this background, of course, time will lend the authority of custom and the tradition once established may be intensified and carried far. The Algonkians are old in the forest region. Groups through movement and change of scene may have swung from the communal to the individual method and back again through the vagaries of historic chance. It must be recognized that while we feel the sequence we have indicated must have taken place in the evolution of the family hunting territory system at some point within the forest regions inhabited by the Algonkians; this is not tantamount to the acceptance of the tundra hunters of northern Labrador today as representative of an earlier undeveloped stratum. Indeed it is quite possible that pushing northward into this area of large caribou herds and dearth of localized game, these bands abandoned property concepts acquired in the lower forest reaches where such adjustments

⁵⁴ H. T. Martin (op. cit. p. 136) emphasizes the winter reliance upon beaver as follows: "When . . . the autumn came, and passed rapidly into the severe winter experienced in nearly the whole of the 'Indian-Beaver' Territory, when the little vegetation that remained was shrouded under a deep covering of snow, when migratory birds, beasts and fishes had abandoned their former haunts, then the Indian looked on the beaver colony as a providential arrangement to supply his wants."

had survival value. Doubtless such reversals of sequence have taken place more than once. Our only contention is that basically the concept of land as a free good must have underlain at some point the rise of the family held tract. Once the latter development takes place, of course, it may, as in the case of any other cultural element, be spread by diffusion among like peoples facing similar environmental necessities. It will not survive or be accepted where communal hunting of migratory game is the chief mode of subsistence. But the very fluidity of the adjustment itself suggests its intimate and sensitive reaction to factors far more heavily natural and environmental than traditional. Such is the nature of the schematized outline, which, for convenient visual purposes we have

appended to this paper as an interpretation of the possible general trend of development of this institution throughout the northern woodland. And just as sensitively ecological, it is our firm belief, will prove to be the effect of environment upon land ownership concepts among the other lower hunters who have been less fully investigated at the present time.

With this interpretation in terms of natural background we can more readily cast aside that dubious schematism which persists in viewing the lower hunters as the representatives of an early and primitive collectivism. Instead, we are coming to view these hunters and seed-gatherers as we actually find them—men meeting a variety of environments in variable ways, and diverging accordingly in cultural response.

ELECTRON-ELECTRON COLLISIONS IN THE PRIMARY ENERGY RANGE FROM 1.3 TO 2.6 MILLION ELECTRON VOLTS

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ABSTRACT

The absolute value of the electron-electron scattering cross-section is studied by observing the production of energetic side branches by primary electrons of kinetic energy T_p . The quantity measured is the number of side branches with energy greater than a chosen value, T_0 , and less than $0.57 T_p$. We employed 343 meters of electron track, with primary energy between 1.3 and 2.6 MEV. The observed numbers of side branches agree with those calculated by Möller's formula, within the limits of error due to experimental difficulties and statistical fluctuations. The ratio, R , of the observed and calculated cross-sections comes out as follows:

T_0 in EKV	R
20.....	1.07 ± 0.09
30.....	0.99 ± 0.11
40.....	1.04 ± 0.12

The Möller formula is essentially correct for the primary and secondary energy ranges considered here.

I. INTRODUCTION

THIS paper is concerned with absolute measurements of the electron-electron scattering cross-section. The problem is to determine the number of side-branch electrons with energy greater than some arbitrary value, T_0 , which are produced per unit length of the track of a fast primary electron. There are two methods for measuring the amount of energy transferred in such electron-electron collisions, occurring in the gas of a cloud-chamber. The first is to determine the energies of the side branches, or secondaries, by measuring their ranges. When the energy of a secondary is 20 electron kilovolts, its range in air at normal temperature and pressure is about 8 millimeters. In this paper secondaries with energies equal to or superior to 20.3 EKV are studied. Since the range-energy relation is accurately known from experiments for the range 20 to 60 EKV, this method has been employed for the work about to be described. The second method of investigating electron-electron collisions, used by Champion,¹ is to

measure the curvature of the primary track and the angle, θ , through which it is scattered in the collision process.

Prior to recent work by Hornbeck and Howell² in this laboratory, the experimental findings were in a contradictory state and covered only a restricted range of primary energies, as we shall see below. The present investigation is a continuation of their work, with the objectives of decreasing the statistical errors and of increasing the accuracy of all the measurements involved.

A. Theory.—We are now in possession of a relativistic theory of the electron-electron cross-section which should yield correct results if the Coulomb law of force is correct at all distances. This theory, due to Möller,³ includes the effects of exchange and retardation of potentials, to terms in $(v_p/c)^2$, inclusive, v_p being the velocity of the incident electron. J. J. Thomson gave a formula for this quantity on the basis of non-relativistic mechanics. What we require here is the cross-section, $S(T_1, T_2)$, for an energy transfer between T_1 and T_2 . If an electron of kinetic energy T_p and velocity v_p strikes a free electron at rest, the result is

$$S_e(T_1, T_2) = \frac{2\pi e^4}{mv_p^2} \left(\frac{1}{T_1} - \frac{1}{T_2} \right), \quad (1)$$

where e is the charge, and m the rest mass.

In the range of secondaries considered here, and for scattering in gases of low atomic number, corrections for the kinetic energy and binding energy of the atomic electrons are negligible. A side branch of energy T may be formed either by an atomic electron or by a primary which has lost energy $T_p - T$. Since it is impossible to distinguish between these cases, we agree to designate the energy of the slower electron at T . Thus, T is always less than $T_p/2$. As a convenient mode of speech, the branch of higher energy will be called the scattered primary, and

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¹ Champion, *Proc. Roy. Soc. A*, **137**, 688 (1932).

² Hornbeck and Howell, *Proc. Amer. Philos. Soc.*, **84**, 33 (1941).

³ Möller, *Annalen der Physik*, **14**, 531 (1932).

the branch of lower energy will be called the secondary. With these conventions, the cross-section for the production of a secondary with energy greater than T , according to classical mechanics, is

$$S_c(T, T_p - T) = \frac{2\pi e^4}{mv_p^2} \left(\frac{1}{T} - \frac{1}{T_p - T} \right). \quad (2)$$

On the basis of non-relativistic theory there is no upper limit to v_p , and for relativistic values of T_p , formula (2) differs widely from Möller's formula. However, if we use for v_p the correct value instead of the non-relativistic one, formula (2) becomes a fairly good approximation to Möller's result over the whole energy domain considered here, and it is very useful in making rough estimates of the cross-section. As v_p approaches its limiting value, c , the cross-section becomes practically independent of T_p . For convenience, we introduce the symbol $A = T/T_p$. (If the two electrons were distinguishable, this would be the fraction of the kinetic energy transferred to the secondary.) The cross-section (2) decreases with an increase in A , becoming zero for A equal to 0.5; because of the convention above, there are no "secondaries" with energy greater than $0.5T_p$. Primary and secondary energy ranges that permit cloud-chamber studies are, therefore, limited, and it is necessary to choose ranges such that a reasonable number of events suitable for measurement can be accumulated.

Möller's more exact formula applies when T is large compared with the binding energy of an atomic electron and small compared with T_p , so it is suitable for use in discussing the present results. Integrating his differential cross-section from an arbitrary lower limit T_0 up to $T_p/2$, the cross-section for production of a branch with energy between these limits is

$$S(T_0, T_p) = \frac{2\pi r_0^2}{\beta_p^2 T_0} \left(\frac{1 - 2A_0}{1 - A_0} \right) \times \left[1 - (1 - g)A_0 \frac{1 - A_0}{1 - 2A_0} \log \left(\frac{1 - A_0}{A_0} \right) + gA_0(1/2 - A_0) \left(\frac{1 - A_0}{1 - 2A_0} \right) \right]. \quad (3)$$

Where $\beta_p = v_p/c$; $A_0 = T_0/T_p$; $g = (\gamma - 1)/\gamma^2$; $\gamma = (1 - \beta_p^2)^{-1/2}$, and $r_0 = e^2/mc^2$. Here the energy is in mc^2 units, and the constants employed are the same as those used by Hornbeck

and Howell, viz., $2\pi r_0^2 = 4.983 \times 10^{-26} \text{ cm}^2$, and $1 mc^2 \text{ unit} = 0.5113 \text{ MEV}$.

The expression outside the square brackets is equivalent to Thomson's formula, if the above mentioned relativistic correction for the change of mass in velocity is made in the latter. The second and third terms in the bracket represent the effects of retardation of potentials and quantum-mechanical corrections. For the range of A -values employed in this work, these two terms alter the cross-section only about 1.3 per cent.

B. Previous Work.—Employing the second method mentioned above, Champion studied the distribution in angle of beta particles scattered by electrons in nitrogen gas, covering the primary energy range from 0.4 to 1.1 MEV. For most of the 250 events studied, however, the primary energy was less than 0.66 MEV. The observed number of branches was 8 per cent lower than the number predicted by Möller's formula, a satisfactory agreement, considering statistical fluctuations.

Williams and Terroux⁴ investigated the secondaries produced on 18 meters of track in oxygen, by primaries having energies from 0.13 to 1.6 MEV. In their work the total number of branches with energies greater than 7.5 EKV was 72. In comparing the data with the predictions of Thomson's formula, the only one available at that time, the ratio, R , of the observed number of events to the calculated number was used. In going from the lower limit of the primary energy to the upper limit, the value of R increased from 1.4 to 2.8.

Hornbeck and Howell, desiring to explain the large discrepancies between the results of Champion and of Williams and Terroux, studied secondaries produced by electrons of energy between 0.7 and 2.6 MEV. Their work was divided into two parts. First, the effect of primary energy upon the cross-section was studied; the energy of each primary was measured, and secondary energies, from 12 EKV up to the highest value encountered, were determined by range measurements. The results show that in the range they covered, the cross-section varies only slightly with primary energy.

In the second part of their investigation, pri-

⁴ Williams and Terroux, *Proc. Roy. Soc. A*, **126**, 289 (1929-1930). See also Howell and Hornbeck's discussion of an interesting experiment carried out by Williams, *Proc. Roy. Soc. A*, **128**, 459 (1930), using primaries of energy 20 EKV.

primary energies were measured only when there was doubt as to whether the primary was in the region being studied. In order to reduce the percentage error in range measurements, only secondaries with energies greater than 20 EKV, or range greater than 0.8 cm, were included. The results are shown in Table II, together with our own data. A value of R in Table II is the ratio of the number of events observed to the number calculated by formula (3). The limit of error given with each value of R is the standard deviation associated with the random occurrence of secondaries along tracks; it does not include any allowance for instrumental or personal errors. The data, in the second column of Table II, indicate a slight excess of observed events over the number calculated by the Möller formula for low values of T_0 . Hornbeck and Howell mention two systematic errors which would increase the value of R . They are: (1) inclusion of slow stray electrons, occurring on or near the primary track, some of which cannot be distinguished from genuine secondaries; and (2) inclusion of tracks which are formed before the chamber expands, when the gas is 1.13 times as dense as it is after the expansion. They estimate that these errors could cause a spurious increase of about 2.8 per cent in the observed cross-section. Table IV gives results corrected for these errors. They also discuss random errors and systematic errors of unknown sign which could cause a resultant error of about 7 per cent. They conclude that their data substantiate the essential correctness of the Möller formula and indicate that the results of Williams and Terroux cannot be correct. According to a private communication from Professor Williams, the same conclusion has been arrived at by Williams and Cameron, from unpublished results which place the value of R at 1.2.

C. Nature of the Present Work.—The present work is a continuation of the second part of the Hornbeck-Howell experiments. It is an endeavor to check more accurately the cross-section for electron-electron collisions in the primary energy region from 1.3 to 2.6 MEV. In the work of both Williams and Terroux and Hornbeck and Howell, it was found that the values of R were greater than one for low values of T/T_p and slightly less than one for high values of this ratio. The following influences, to varying degrees, may be responsible for this: unfavorable statistical fluctuations in the occurrence of events; inclusion of slow electrons produced in

the gas so close to the track that they cannot be distinguished from bona fide secondaries; inclusion of pre-expansion tracks; inaccuracy in range measurements; straggling of secondaries; and errors in the range-energy curve. It is desirable, therefore, to have a larger body of data with special emphasis placed on high values of T/T_p , in order to reduce the statistical fluctuations to a value comparable with, or less than, the resultant experimental errors. Improvements in the technique of measuring ranges of secondaries and in the criteria for selecting tracks have been attained. Also, we have determined more accurately the corrections for the two systematic errors mentioned above, by observations more extensive than those of Hornbeck and Howell. In this way, the influence of these two systematic errors on the final results can be practically eliminated.

II. TECHNIQUE

A. Measurement of Energies.—As in the work of Hornbeck and Howell, the primaries were recoil electrons produced in the walls of a nitrogen-filled cloud-chamber, by gamma-rays from a well-aged mesothorium source. As in their case, our measurements were made on a large collection of photographs taken by Dr. C. C. Jones, in a field of 1200 gauss. The stereoscopic viewing apparatus described by Jones and Ruark⁵ was employed. Primary energies were determined by radius measurements, and secondary energies were obtained from ranges by means of von Droste's⁶ curve, based on all data, for several gases, available up to the time of his paper. It covers the range of energies up to 50 EKV. The inaccuracies in this curve are thought to be less than 4 per cent for reasons explained by von Droste and by Hornbeck and Howell.

Two methods were employed for measuring ranges. We used a glass centimeter scale for those tracks which were nearly straight and nearly in the plane of the ground glass viewing screen. The method for measuring the component of the track length perpendicular to the screen has been described by Jones and Ruark. For secondaries which experienced abrupt changes in direction, or which consisted of spirals of short radii, or which were otherwise difficult to measure, a piece of No. 27 bare copper

⁵ Jones and Ruark, *Proc. Amer. Philos. Soc.*, **82**, 253 (1940).

⁶ von Droste, *Z. Phys.*, **84**, 17 (1933).

wire was placed on the screen and bent into the shape of the projected track-image. Thus, it became, as nearly as could be determined, a replica of the projected image. The wire was held on the screen while viewing the track image stereoscopically, and thus if the image was not in the plane of the screen, the wire still could be made to approximate the shape of the track. By straightening the wire one could get an accurate measurement of the projected length. If the component of track length perpendicular to the screen was appreciable, it was, of course, determined. The wire method is more accurate and more objective than that used by Hornbeck and Howell, in which the track length was approximated by a series of chords. In their measurements the scale itself was applied to the track image. If the energy happened to lie near the boundary of two secondary groups, there might be a personal tendency to put the track in one group rather than the other. In our method, the length of the projection is unknown until after the wire has been applied and its length has been measured. Since errors in the range measurements are important, especially for 20 EKV branches having a length of about 0.8 cm, each secondary was measured independently at least twice, by each of two observers. Where the results of the two observers were in close agreement, the average of the results was taken. In the few cases in which, due to complex shape or unfavorable position of the secondary, the two results did not agree within 5 per cent, the measurements were repeated at least three times by each observer, and an average of the several measurements was taken. Of course, this careful repetition was necessary only when the secondary was near the boundary of an energy group. To make the final results still more objective, no summary of the secondaries or calculation of the expected number of events was made until all measurements were complete.

B. Criteria for Selection of Tracks.—In spite of precautions in taking the electron photographs obtained with a gamma-ray source, some diffuse pre-expansion tracks and some weak post-expansion tracks due to "late" electrons, will always be present. Some tracks will lie in regions unfavorable to accurate measurement and should be excluded. It is essential to adopt objective criteria as to the inclusion or exclusion of tracks before the measurements are begun. Such criteria should be so chosen that the number of decisions required is reduced to a minimum.

Our criteria, which differ somewhat from those of Hornbeck and Howell being based on their experiences and difficulties, were as follows:

1. Only primaries which have h/c less than 0.3 were taken; where h is the distance parallel to the field, between the ends of the measured arc of the track and c is the chord length. Only a few tracks were excluded by this criterion. Since the length of a track having h/c less than 0.3 differs only slightly from the length of its projection on the ground-glass viewing screen, very little error would be incurred even if no correction were made for this difference between the true length and the projected length. However, measurements were made on 150 tracks in order to determine the magnitude of this error, and finally a correction was applied to the total projected track length.

2. In order to minimize errors in total track length, no primary of length less than 5.0 cm was taken.

3. To minimize the percentage of pre-expansion tracks included and to increase the accuracy of the curvature measurements, tracks the images of which on the viewing screen were wider than the arbitrary value of 0.8 mm were excluded. The width was compared with a standard ink line ruled on a transparent sheet.

4. Portions of primaries which were obscured by other tracks so that secondaries might be missed entirely, or misinterpreted, were not included. The application of this criterion was not often necessary; however, to avoid the inclusion of tracks which might falsify the results, the pictures were first projected non-stereoscopically in quick succession, and the frames containing obviously undesirable clusters of tracks were eliminated.

5. In the case of primaries which became gradually faint within 2.5 cm of the chamber wall (distance measured perpendicular to the wall), the track was considered to extend to the wall, for it is probable that any slow secondary produced in this region could be detected because of its density of ionization, in spite of the slight defect of vapor density responsible for the faintness. To get an estimate of the error that could be incurred if this assumption were partially erroneous, the sum of the lengths of these faint portions was found for 100 meters of track. The added track length due to their inclusion was only about one-half per cent of the total. Tracks that became faint farther than 2.5 cm from the wall were included, but only the portions that could be distinctly seen were used; these tracks constituted less than one per cent of the total track length.

6. The primaries and secondaries must be of the same age, as far as can be determined visually.

7. The length of a secondary was measured from the middle of the primary track to the center of the droplet or cluster of droplets on the end of the secondary.

III. RESULTS

The theoretical cross-section changes only about 1.3 per cent, as one varies the primary energy over the entire range studied here, but to increase the accuracy of the calculated values as much as possible, the energies of 200 tracks were measured in order to determine the energy spectrum for this body of data. The tracks were divided into four energy groups and a hodograph was plotted showing the fraction of the total track length lying in each energy group. The results of the survey are shown in Table I. The

TABLE I
PRIMARY ENERGY SPECTRUM

Energy Group MEV	Fractional Part of Total Track Length in Group
1.30-1.64	0.322
1.64-1.98	0.443
1.98-2.32	0.182
2.32-2.60	0.053

theoretical cross-section is a weighted mean calculated by means of this hodograph.

On a total of 343 meters of primary track, 180 secondary electrons were found. In presenting results of this kind, the events can be classified in either of two ways. One may count the number of secondaries with energies in certain arbitrary domains, T_1 to T_2 , T_2 to T_3 , etc. Alternatively, one may count the number of secondaries with energies superior to T_1 , T_2 , and T_3 (equal to 20.3, 31.4, and 42.2 EKV in this work) respectively. We have used the latter method for a reason made clear by the following example. If a secondary with energy of 30 EKV were wrongly assigned to the group 31.4-42.2 EKV, the error would take double toll, so to speak, for the numbers in the group 20.3-31.4 and 31.4-42.2 EKV would both be falsified. However, using the second plan, the number in the group "20.3 EKV and up" would not be affected by this error; furthermore, the percentage effect on the group "31.4 EKV and up" would be smaller than the effect on the group 31.4-42.2 EKV employed in the first method of presentation. Accordingly, Table II shows the number of secondaries having an energy greater than a chosen lower limit T_0 , as a function of this limit. Due to slightly different electron densities, our limits of energy are slightly different from those of Hornbeck and Howell. The

TABLE II
VARIATION OF R WITH ENERGY OF SECONDARIES

Author	Lower Energy Limit (EKV)	Calculated No. of Events	Observed No. of Events	R
Hornbeck- Howell	20.5	88.3	107	1.21 ± 0.12
	31.6	56.4	63	1.12 ± 0.14
	42.7	40.9	35	0.86 ± 0.15
Shearin- Pardue	20.3	162.0	180	1.11 ± 0.08
	31.4	103.3	105	1.02 ± 0.10
	42.2	76.0	81	1.07 ± 0.12

uncertainties assigned to the R -values are those due to statistical fluctuations alone.

IV. DISCUSSION OF RESULTS

The more important errors encountered are as follows:

1. *Strays*.—We studied all stray electrons produced in the gas of the chamber, occurring in several frames of each film used in the present work. It was assumed that one could distinguish between a stray and a bona fide secondary if the stray lay entirely outside a cylinder of 2 mm radius around the primary, a liberal estimate. For a secondary of energy greater than 40 EKV, one can ordinarily tell from its curvature, whether it ends or begins on the primary, thus reducing by one-half the value of the error in this energy range. Also, the deflection of the primary can be observed for secondaries of energy greater than 30 EKV, unless the secondary is ejected in a direction nearly parallel to the line of sight. Furthermore, each genuine relatively slow secondary should leave the primary nearly at right angles; in practice it may be scattered close to the primary, but occasional troubles in recognizing a true secondary caused by such scattering, will be pronounced only for branches in the energy range 20-30 EKV. Taking these factors into consideration, all strays in the frames studied were counted and classified according to their energies. The number of strays, N_s , with energies lying within a given energy range, to be expected on the average track length found in one frame, is given by

$$N_s = N(v/V), \quad (4)$$

where v is the total volume of cylinders 2 mm in radius surrounding the tracks on one frame; V is the volume of the cloud-chamber; and, N is

the number of strays, in the given energy range, per frame. Table III shows the results.

TABLE III

Lower Energy Limit of Group (EKV)	Percentage of Spurious Secondaries
20.3	1.49
31.4	0.66
42.2	0.41

2. *Pre-expansion Tracks*.—Hornbeck and Howell estimated that the error in the cross-section due to the inclusion of pre-expansion tracks is less than 3 per cent. The error is probably about 2 per cent, and is such as to increase the value of R .

3. *Range Errors*.—Range measurements for secondaries near the lowest energy limit are more difficult to make than those at the other limits; thus the personal and instrumental errors in measurements at the lowest energy limit are greater than those at the other limits. We believe that in measuring an individual 8 mm track the average error is not more than 0.4 mm. This would give a maximum error in the cross-section of unknown sign, amounting to 2.5 per cent. Even if a systematic error of 0.4 mm existed in the case of all branches belonging to the group for which T_0 is equal to 20.3 EKV, the error in the measured cross-section could be only 2.5 per cent. Considering the compensation due to the random nature of the errors in range measurements, a liberal estimate of the effect on the cross-section is 1.5 per cent.

4. *Straggling Errors*.—Calculations were made to estimate the error in the number of events observed in a given energy range, due to straggling of the secondary electrons. For the purpose of this calculation, the 20.3 EKV limit was considered. Assuming that the electrons of a given energy follow a Gaussian distribution, with a half-width at half-maximum amounting to 26 per cent of the range, the total number of secondaries with energies less than 20.3 EKV, that would have ranges greater than the mean range, R_0 , for 20.3 EKV electrons, was calculated numerically. Likewise, the number of secondaries of energy greater than 20.3 EKV but with ranges less than R_0 was calculated. Formula (1) was used to determine the expected number of secondaries in a range dT ; the relativistic values of v_p and T_p were employed. The results show that for the 343 meters of track

considered here, 9.2 electrons with energy less than 20.3 EKV should be affected by straggling in such a way that they would be attributed energies greater than 20.3 EKV; 9.0 electrons with energy greater than 20.3 EKV should be attributed energies less than that value. Because of this compensation, the systematic effect of straggling on the cross-section should be negligible in our work. If the very unfavorable case were taken, in which 9.2 events straggled to lower energies, the error in the observed cross-section would be 5 per cent. We believe 2 per cent is a liberal estimate for straggling error.

5. *Range Energy Curve*.—We believe that the error in energies read from this curve is less than 4 per cent.

To summarize, we have discussed five important sources of error. The personal and experimental error in measuring the ranges of the secondary electrons, the straggling error, and the error in the range-energy curve are of unknown sign; compounded in the usual way, the resultant is 4.7 per cent. The systematic errors due to inclusion of stray events and pre-expansion tracks can be subtracted. The results, after correction for these two errors, are shown in Table IV, together with comparable values

TABLE IV
CORRECTED RESULTS

Approximate Lower Energy Limit (EKV)	R Hornbeck and Howell	R Shearin and Pardue
20	1.18 ± 0.14	1.07 ± 0.09
30	1.09 ± 0.16	0.99 ± 0.11
40	0.84 ± 0.17	1.04 ± 0.12

given by Hornbeck and Howell. The limits assigned are the resultants of fluctuation error and instrumental and personal errors of unknown sign.

Of the work preceding this paper, only that of Hornbeck and Howell will be discussed here in connection with our results, because the results obtained by Williams and Terroux have been shown to be erroneous, and Champion's results, for much lower primary energy, are in fair agreement with theory. As pointed out above, several improvements have been made over the Hornbeck and Howell experiment, by taking advantage of their experiences and difficulties. These improvements have enabled us to obtain

results that should be more accurate than theirs. A part of the discrepancy between the Hornbeck and Howell results and theory is probably due to unfavorable statistical fluctuations, particularly in the case of the second and third energy groups where the value of R is based on a small number of events. Their results and our own do not indicate any definite failure of theory when the possible errors, statistical and instrumental, are considered. The decrease in the R -values as T_0 increases, found by Hornbeck and Howell, does not appear in our results. We conclude that the Möller formula is essentially correct for the ranges of primary and secondary energy we have covered. We wish to emphasize the importance of thorough tests of this formula, the only one in which the interaction of two

similar fundamental particles has been calculated with perfect symmetry, in accordance with the spirit of Breit's considerations.⁷ Experiments for much higher values of T_0/T_p , and for T_p values in the cosmic ray domain, are being prepared, but will be time-consuming. We express our appreciation to The American Philosophical Society for a grant to Dr. Arthur E. Ruark which made this work possible, and to Dr. Creighton C. Jones for permission to use the photographs from which these measurements were made. We are grateful to Dr. Ruark for discussions of theory and of the experimental procedures.

November 7, 1941

⁷ *Phys. Rev.*, **34**, 553 (1929).

THE MICROSCOPY OF MAMMALIAN HAIR FOR ANTHROPOLOGISTS*

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ABSTRACT

An attempt is made to develop a technique for identifying hairs and wools from various types of materials recovered during archeological work in North America and primarily in the Southwest. In this first section keys, brief descriptions and drawings are presented for all of the genera of *Carnivora* found north of the Mexican border. These aids are not proposed to supplant direct comparison with known material but to aid the archeologist in selecting material for comparison.

INTRODUCTION

NUMEROUS studies of the microscopy of human hair have been made for the use of anthropologists. With continued refinement of techniques these studies have tended to eliminate any necessity for microscopic examination of human hair specimens in routine anthropometry. While it may prove that there are differences that set apart the various races and sub-races that may be based upon the microscopy of hair, it has been fairly well proven that the race of an individual cannot be determined with certainty from the microscopic structure of the hair. Kneberg¹ has shown the old idea that the texture of the head hair was definitely associated with the cross-section index to be erroneous. She has also demonstrated that the form of the cross-section is not a racial characteristic. Hausman² had previously shown that the cuticular scales and medullary structure are directly related to the diameter of the hair shaft, and his student, Miss Wynkoop,³ has shown that age has little or no bearing on the microscopic structure. Work under way by the present author seems to indicate that there is little additional information gained from a microscopical examination of hair gathered from ten different parts of the body of a "normal" individual. Thus, so far as man is concerned, the anthropologist need pay little attention to other than the gross aspects of the hair. There may be some benefit derived from the study of the microscopic structure of patho-

logic hair. This is being investigated by several workers.

The microscopy of the hair of other mammals may be a very useful tool for the archeologist and ethnologist. Primitive peoples have used wool derived from many sources and bits of fur have been extensively employed by them. It is of interest to know the animal source of the hair and hide so employed. To my knowledge there has been no lengthy paper devoted to the microscopic structure of hair from a taxonomic point of view other than Glaister's.⁴ Unfortunately the value of this contribution is negated by the poor reproductions illustrating it. Many of Hausman's papers are helpful and contain considerable material but none of them may be used as a basis for the determination of the source of a hair sample.

For the past twenty years I have dabbled with the micro-structure of hair from a taxonomic stand-point. Most of this was purely to satisfy a personal curiosity. More recently I have been called upon to determine the sources of samples of yarns recovered from archeological sites and a variety of other materials of ethnic value. Three years ago through the encouragement of Dr. A. V. Kidder of the Carnegie Institution and with partial financial aid from the American Philosophical Society I embarked upon this venture. At the beginning I had hoped to be able to reduce to a purely objective study the technique for determining the species from which a given group of hairs came. In other words to build a simple key to the characteristics. In this I have been only partially successful. While the keys may function properly for me I have no illusion that they are universally good. The keys may help eliminate some genera but the only certain way to study an unknown is to compare it minutely with material from known sources. The drawings which have been pre-

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¹ *Amer. J. Phys. Anthropol.*, xx, 51-69, 1935.

² *Amer. J. Phys. Anthropol.*, viii, 173-178, 1925.

³ *Amer. J. Phys. Anthropol.*, xiii, 177-187, 1929.

⁴ "A Study of Hairs and Wools Belonging to the Mammalian Group of Animals, Including a Special Study of Human Hair Considered from a Medico-Legal Aspect." Egyptian University. Faculty of Medicine; Publication no. 2. Cairo-Misra Press; 1931, pp. 188, 145 pl.

pared for every genus of mammal found north of the Rio Grande—except the *Pinnepedia* and *Celacea*—will further help to limit the possibilities in the identification of material of unknown source.

TECHNIQUES

The techniques employed for preparing a sample are simple. The specimen is first washed in alcohol-ether, dried, and then cleared in xylol for balsam mounting or mounted dry without clearing. For dry mounting I find small strips of Scotch Tape very convenient for fastening the cover-glass to the slide. Dry mounted slides are best for the study of the cuticular scales, balsam mounts for the medullary structure and pigmentation. Unless the cells of the medulla are impregnated with balsam that region will defy study. Impregnation will be assured if one or two hairs are cut into short lengths. Drying the slides in an oven at 37–40° C. is very helpful. A 40X objective worked with a 10X ocular is an admirable combination for most study. Occasionally oil-immersion is necessary for the study of pigment granules. While transmitted light such as is necessary for the study of the medulla and pigment will occasionally detail the scales, a beam of light from one side and just above the horizontal is best suited for their study. It is often helpful to use a lower powered objective and higher powered oculars for the scales since that will give a better depth of field.

THE STRUCTURE OF HAIR

Reduced to the simplest terms hair is a tube. The walls of the "tube" are solid and termed the cortex, the bore of the "tube" is called the medulla and is usually filled with air cells. The outer surface of the "tube" is sheathed with overlapping scales called cuticle. In cross-section hairs present a variety of forms from circles

to strongly flattened ellipses or elongate ovals, or they may be triangular or polygonal. These forms do not seem to be constant and with a few possible exceptions are probably of no taxonomic value. The cross-section of a single hair shaft may be quite variable or it may be reasonably constant throughout its length. Certain externally applied pressures will change the shape of the cross-section, i.e. twisting for yarn or compression in an envelope. Most hair shafts show some variation in diameter throughout their length. The base is usually of less diameter than the mid-section and the tip may taper off to practically nothing or be blunt. The greatest diameter may be approached gradually or within a very short distance. Reference to Figs. 1 to 3 will visualize some of the changes found throughout the length of the shafts of some hairs. All of these figures are drawn from measurements taken from actual specimens. The first is a "normal" hair from the back of a Black Bear. The second is a type found in the *Cervidae*. The specimen is from the flank of a Pronghorn and shows the modified structure to a high degree. This will be further discussed in dealing with *Antilocapra*. The third figure represents a condition common among the *Mustelidae* and developed to a high degree in the Otter, *Lutra*. References to diameter in the text are made to definitely stated regions—usually the base or the widest portion of the hair.

The scales of the cuticle are of considerable importance in the taxonomic study of hair. The nomenclature for the various forms of cuticular scales was established by Hausman.⁵ It needs no further embellishment for this paper. The ratio of the length of the free proximo-distal portion of the scale and the diameter of the shaft is called the scale index, $\frac{F}{D} = S.I.$ This

⁵ *Amer. Nat.*, 44, 496, 1920.



FIGS. 1, 2, 3.

index usually varies inversely with the diameter. So scale indices may be applied only when hairs of the same diameter are being compared. The indices may be of some taxonomic importance but are so variable that this is yet to be fully established. The indices stated in the text are averages taken over a distance of 400 microns along the margin of the optical section (Fig. 4).

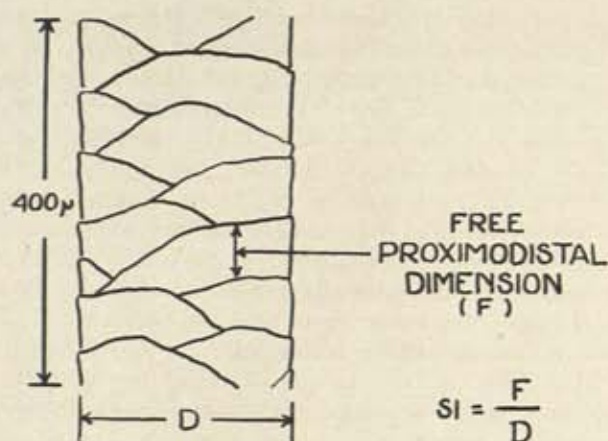


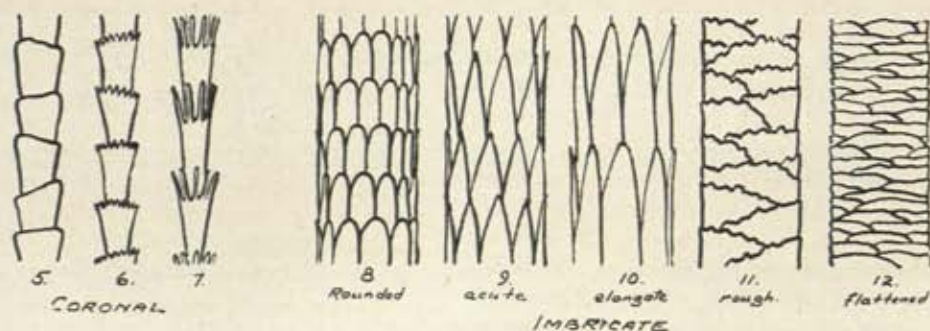
FIG. 4.

The types of cuticular scales, after Hausman, are shown in Figs. 5 to 12 and little further description is necessary. Coronal scales, a peculiar form which completely encircles the shaft, are characteristic of the *Chiroptera*. They are found rarely in the other orders and then only on the thinnest fur hairs and not then are they the dominant form. The outline of the free margin of the scales is often helpful taxonomically as is the mode of imbrication. Occasionally the scales are pigmented.

The cortex of the shaft constitutes its real body. Hairs in which this portion constitutes a minor part of the diameter are usually brittle—

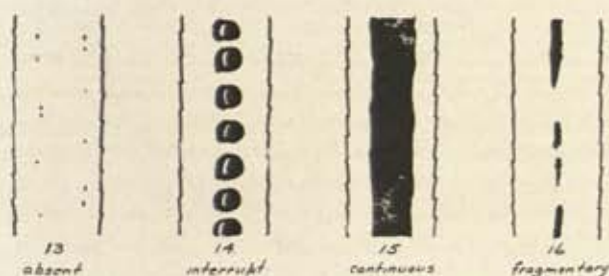
the hair of the deer is a good example of this. An extremely thin cortex plus a medulla filled with large cells is characteristic of some of the *Artiodactyla*, especially the *Cervidae*, etc. The proportion of the shaft occupied by cortex and medulla varies throughout the length of the shaft but within limits is constant enough for a given region to be of considerable diagnostic assistance. At the extremes of the hair shaft the cortex may compose the entire shaft. In rather rare instances this is true throughout the shaft. Within the cortex occur granules of pigment, the size, shape and frequency of which are of importance for the diagnosis of certain genera and species. There may also be a diffuse stain with or in lieu of pigment granules. Not to be confused with pigment granules are tiny "flaws," elongate air bubbles, called fusi. To the practiced eye these are not difficult to recognize. They occur more frequently in the hairs of some species than of others.

The medulla is usually filled with thin-walled cells of air. These cells vary a great deal in size and shape. Their general appearance is a helpful taxonomic character. They may be globular or flattened, they may be remarkably uniform or quite irregular or varied. They may extend completely across the medulla or only part way. They may appear to be loosely or closely packed. They may be so compressed as to appear like thin plates. When they are filled with air they make the medulla appear black under the microscope. Their full study requires that they be impregnated with the mounting medium. Pigment granules may or may not be present in the medulla. The granules may be in the cells but much more frequently they are packed into the interstices of the air-cells. The characteristics of the pigmentation are worth noting. Many of the *Rodentia* are immediately recognizable by it.



Figs. 5-12. Types of cuticular scales.

The form of the medulla is of importance in some genera, Figs. 13 through 16 show the four major types, after Hausman.



FIGS. 13-16.

THE TYPES OF MAMMALIAN HAIR

Broadly all hair can be divided into two classes. These are the protective hair and fur hair. The coarse, outer-hair is called the protective hair and the fine, often woolly, under-hair is called the fur hair throughout this paper. It is always to the advantage of the investigator to have bits of both types in exploring the possibilities of an unknown. Certain other, rather specialized kinds of hair are to be found on mammals—whiskers, bristles, mane and tail, and quills. These are not included in this paper. Their occurrence in the handicraft of primitive America is restricted to the easily recognized quill of the porcupine and recently the use of the tail hairs (and probably mane hairs) of the domestic horse.

PROCEDURE FOR EXAMINATION

Perhaps it is not amiss to insert at this point a brief outline of the procedure that I use in examining an unknown. A careful study of the gross aspects of the sample will usually eliminate many genera. For instance, with few exceptions, hairs an inch or more in length are not found among the *Rodentia*, while among the *Artiodactyla* hairs under an inch in length are equally rare except on the face. The color of the hair will often open up a lead but this is one to be followed with caution since many species bear hairs of a variety of colors. After gathering as many leads for the gross examination as possible I turn to the prepared slides and examine the balsam mounts first. These I examine *in toto* and note the general structure of the medulla, the gross diameter at the widest part of the specimen and the diameter of the medulla at the same point. At this time I also pay close

attention to the shape of the longitudinal section. In general this will help in allocating any specimens from the *Carnivora* and especially from the *Mustelidae*. I also measure the scale index at this time as already outlined (see Fig. 4). Next I turn to the dry mounts and using flat, reflected light in place of the usual transmitted light study the contours of the scales. These are usually more easily studied in the basal regions of the hair shaft than the distal. This completes my first microscopic examination.

The data accumulated in the first study I use to select the slides of known material for comparisons. On pages 254, 255 I have gathered the information regarding the *Carnivora* of North America that will be useful in making these selections for that group. When the probabilities have been reduced to three or four genera I then carefully check through the data I have concerning them and the unknown with the aim of further elimination. Finally I compare the various parts of the unknown with the same parts of a specimen of known origin and approximately the same diameter. Such an examination is best done with a comparing microscope. This will usually eliminate all but one genus. Determination to species is then carried out in a similar manner but is often very difficult.

ACKNOWLEDGMENTS

I bring these introductory remarks to a close with a feeling of debt to many people. Dr. L. A. Hausman's pioneering in the field and his careful development of a standardized nomenclature for the structures of animal hair leaves all who carry on further work with a great respect for his studies and published papers. I owe a personal debt of thanks to Dr. E. R. Warren, who has freely given me access to his extensive collection of western mammals, to Dr. A. M. Bailey and his staff at the Denver Museum and to Dr. Herbert A. Anthony and his staff at the American Museum of Natural History for assisting me in filling out the series of samples necessary for this study. I cannot omit from this group Miss Georgia Minshall⁶ who prepared over 6000 slides for this study and who undertook to work out the characteristics of the hairs of the *Artiodactyla* as part of her work for her Master's degree at Colorado College.

This, the first of a series of similar papers, is devoted to the *Carnivora*. I have broken away

⁶ Now Mrs. H. Weston Robbins.

from a pure taxonomic order of treating the orders of mammals since the majority of specimens that I have been called upon to pass judgement on are either from the *Carnivora* or *Artiodactyla*. These will be treated first and the orders that seem to be of less importance to anthropologists later. Within the groups taken up I have and will maintain strict taxonomic sequence and follow Anthony in his *Fieldbook of Mammals*. This handy volume should be in every anthropologist's kit if he plans to make any studies relating to the fauna associated with a recent culture.

CARNIVORA

The carnivores range throughout the entire area covered by this paper. They are represented by twenty genera divided among six families. It is probable that the aborigines used the fur of most of them.

Both protective and fur hairs are always present. There is a great range in the length of the hairs from the shaggy pelage of the *Ursidae* to the smooth coat of some of the smaller *Mustelidae*. Generally speaking the protective hairs are widest distad of the mid-region. In some genera the taper is abrupt (*i.e.* *Lutra*) in others almost imperceptible (*i.e.* *Ursus*). The hair color varies from white to black, and the pigment granules vary accordingly from none to many.

Among the *Mustelidae* the cuticular scales of the fur hairs are highly modified in some genera. Among the *Canidae* the scales of the protective hairs are the bearers of helpful characteristics. In general though the scales are rather simple. A medulla is always present, at least in the widest portion of the hair and is continuous in the protective hairs and may be continuous or interrupted in the fur hairs. The medulla seldom constitutes less than 40 per cent of the shaft

Genus	Protective hair									
	Diameter at widest part in microns			Proportional diameter of medulla at widest part of shaft			Scale index			
							Base		Wide part	
	Min.	Mean	Max.	Min.	Mean	Max.	Index	Diam. microns	Index	Diam. microns
<i>Euardos</i>	104	138	190	0.18	0.34	0.42	0.33	110	0.10	170
<i>Ursus</i>	100	163	260	0.09	0.27	0.40	0.16	176	0.10	248
<i>Thalarctos</i>	80	139	200	0.19	0.37	0.50	0.16	50	0.11	160 widest 0.35 128 mid-section
<i>Procyon</i>	100	161	268	0.19	0.38	0.53	0.28	120	0.09	228
<i>Bassariscus</i>	95	170	150	0.60	0.77	0.84	0.78	64	0.16?	100
<i>Martes</i>	72	136	176	0.60	0.67	0.79	1.11	72	0.10	150
<i>Mustela</i>	92	149	176	0.56	0.80	0.87	1.60	48	0.12	140
							0.84	60	0.07	168
<i>Gulo</i>	160	204	264	0.41	0.52	0.64	0.12	96	0.08	176
							0.40	96		
<i>Lutra</i>	235	280	330	0.34	0.53	0.60	0.16	80	0.12	304
							0.43	104		
<i>Enhydra</i>	64	120	208	0.15	0.20	0.22	0.88	92	0.06	200
<i>Spilogale</i>	40	111	204	0.31	0.62	0.79	2.4	24	0.12	84
<i>Mephitis</i>	48	150	248	0.32	0.52	0.80	0.21	74	0.06	172
							0.14	104		
<i>Conepatus</i>	84	189	300	0.34	0.53	0.66	0.15	92	0.06	180
							0.14	120		
<i>Taxidea</i>	160	222	300	0.52	0.75	0.91	0.16	120	0.09	264
							0.30			
<i>Vulpes</i>	108	153	220	0.60	0.74	0.84	0.28	116	0.10	152
<i>Urocyon</i>	140	189	268	0.63	0.74	0.80	0.46	152	0.10	228
<i>Alopex</i>	56	85	132	0.33	0.61	0.76	0.78	52	0.32	88
<i>Canis</i>	156	191	228	0.55	0.69	0.88	0.16	192	0.10	180
							0.21	160		
<i>Felis</i>	132	167	208	0.47	0.62	0.70	0.14	84	0.07	172
							0.42			
<i>Lynx</i>	88	152	184	0.67	0.75	0.83	0.14	88	0.04	176

Genus	Fur hair									
	Diameter at widest part in microns			Proportional diameter of medulla at widest part of shaft			Scale index		Cortical pigment	Medullar pigment
	Min.	Mean	Max.	Min.	Mean	Max.	Index	Diam. in microns		
<i>Euarctos</i>	50	61	76	0.31	0.36	0.50	1.00	40	✓	✓
<i>Ursus</i>	44	77	108	0.12	0.20	0.27	0.50	64	✓	ab.
<i>Thalarcos</i>	44	69	120	0.25	0.36	0.50	0.80	80	ab.	ab.
<i>Procyon</i>	20	32	60	0.00	0.41	0.67	2.40	20	✓	ab.
<i>Bassariscus</i>	20	24	30	0.37	0.55	0.67	1.60	32		
<i>Martes</i>	20	28	36	0.43	0.56	0.67	1.80	20	ab.	✓
<i>Mustela</i>	15	22	30	0.50	0.66	0.75	0.53	28		
<i>Gulo</i>	40	50	76	0.32	0.45	0.54	5.00	20	varies	?
<i>Lutra</i>	12	16	24	0.00	0.16	—	1.70	30		
<i>Enhydra</i>	20	31	56	0.00	0.20	(0.60)	3.20	18	✓	ab.?
<i>Spilogale</i>	16	26	56	0.33	0.41	0.67	0.41	28		
<i>Mephitis</i>	24	37	64	0.14	0.30	0.50	1.30	35	varies	✓
<i>Conepatus</i>	28	46	80	0.00	0.21	0.25	0.46	64		
<i>Taxidea</i>	36	48	60	0.27	0.30	0.47	6.00	12	ab.	ab.
<i>Vulpes</i>	20	26	40	0.60	0.70	0.80	4.00	16		
<i>Urocyon</i>	24	30	40	0.37	0.53	0.62	4.00	20	✓	ab.
<i>Alopex</i>	20	30	60	0.40	0.57	0.69	1.80	36		
<i>Canis</i>	28	55	100	0.28	0.48	0.65	0.75	48	ab.	✓
<i>Felis</i>	28	58	112	0.25	0.42	0.47	1.00	24	ab.	ab.
<i>Lynx</i>	16	27	40	0.37	0.55	0.70	1.40	28	ab.	ab.
							0.70	36		
							1.60	20	ab.	?
							1.00	36		
							1.25	36	ab.	✓
							0.15	96		
							1.30	32	✓	✓
							0.28	48		
							1.05	20	rare	✓
							0.67	24		

diameter except in the *Ursidae*. It is often as much as 75 per cent of that measurement at the widest part of the shaft. The medullary cells vary considerably in size and shape and constitute a good character for some genera. In general there is not a great deal of pigment between the cells of the medulla.

Although it is possible to recognize some of the genera from either a protective or a fur hair several of both are usually required for positive determination.

The following tabulations of gross characteristics that are easily observed and measured may be of assistance in pointing the way to a determination. In no case do these figures apply to single hairs. A satisfactory average figure can

be made from measurements of as few as twenty individual hairs. The examiner must use his own judgement about the validity of any series of measurements he makes on this basis.

A KEY TO THE PROTECTIVE HAIR OF THE *Carnivora*

- Medulla less than 0.4 of diameter of the shaft at its widest part.....1
 Medulla between 0.4 and 0.7 of the diameter of the shaft at its widest part.....2
 Medulla over 0.7 of the diameter of the shaft at its widest part.....3

Section 1

- a. Medulla of clearly defined cells (see Fig. 18).....b
 Medulla of ill-defined cells.....*Procyon*

- b. Cortex free of pigment.....*Thalarchos*
Cortex pigmented.....c
c. Medulla fragmentary in basal region.....*Ursus* *
Medulla usually interrupted in the basal region.....*Euarctos* *

Section 2

- a. Maximum diameter of the shaft less than 100 μb
Maximum diameter of the shaft between 100 μ and 200 μd
Maximum diameter of the shaft greater than 200 μi
b. Cortex free of pigment.....*Alopex* (white phase)
Cortex pigmented.....c
c. Medulla fragmentary.....*Enhydra*
Medulla interrupted or continuous.....*Spilogale*
d. Medulla principally fragmentary.....*Enhydra*
Medulla otherwise.....e
e. Extreme basal portion of this fragmentary.....g
Extreme basal portion of this interrupted.....f
f. Medullary cells at base of hair uniform and globose (see fig. 76).....*Spilogale*
Medullary cells at base of hair irregular in size and shape (see Fig. 45).....*Martes*
g. Basal portion of medulla tapers abruptly.....*Canis*
Basal portion of medulla tapers gradually.....h
†h. Hair is tawny or white and does not show any considerable increase in diameter beyond the mid point.....*Felis*
Hair is black or white and usually shows some increase in diameter beyond the mid point.....*Conepatus* or *Mephitis*
i. Distal portion of the shaft markedly spatulate.....*Lutra*
Not so.....j
j. Extreme basal portion of the medulla is fragmentary.....k
This not fragmentary.....*Lutra*
k. Extreme basal portion of medulla tapers abruptly.....*Canis*
Not so.....l
l. Medullary cells flattened (see Fig. 91).....*Conepatus*
Medullary cells globular (see Fig. 57).....*Gulo*

Section 3

- a. Maximum diameter of shaft over 200 μb
Maximum diameter of shaft under 200 μd
b. Scales elongate at least over most of basal half of shaft.....c
Scales irregular but not elongate.....*Taxidea*
c. Scale index in mid-part of shaft over 0.3.....*Urocyon*
Scale index in mid-part of shaft less than 0.2.....*Canis*
d. Medulla contains many large strongly inflated cells in the region of maximum diameter.....*Lynx*
Such cells absent or very rare.....e
e. Distal portion of the shaft markedly swollen.....f
Distal portion of the shaft not so.....g
f. Medullary cells at the base robust, flattened, often joined together as in a horizontal "H" or "U".....*Martes*
Medulla at the base without distinct cells but deeply indented giving the impression of flattened cells.....*Mustela*

* Note.—These may be readily separated by means of the fur hair (see Figs. 20 and 28).

† Note.—This bracket breaks down badly. Consult the figures and text. The fur hairs of these three genera separate easily.

- g. Basal portion of medulla interrupted.....*Bassariscus*
Basal portion of medulla fragmental.....i
h. Scale index at mid-part of the shaft greater than 0.3.....*Urocyon*
Scale index at mid-part of the shaft less than 0.2.....i
i. Seldom more than two "courses" of cells across the medulla at the maximum diameter.....*Vulpes*
Usually more than four "courses" of cells across the medulla at the maximum diameter.....*Canis*

A KEY TO THE FUR HAIR OF THE Carnivora

1. Shaft diameter greater than 40 μ2
- Shaft diameter less than 40 μ16
2. Pigment and stain present in mid-part of shaft.....3
- Pigment and stain absent in mid-part of shaft.....9
3. Medulla greater than 0.3 of shaft diameter.....5
- Medulla less than 0.3 of shaft diameter.....4
4. Medulla absent.....*Procyon*
- Medulla present.....7
5. Medulla interrupted.....6
- Medulla fragmental.....*Procyon*
6. Scales elongate, no medullary pigment.....*Euarctos*
- Scales usually not elongate, medullary pigment.....*Felis*
7. Medulla interrupted.....*Felis*
- Medulla fragmentary.....8
8. Scale index in basal half less than 0.5.....*Conepatus*
- Scale index in basal half greater than 0.5.....*Ursus*
9. Medulla interrupted.....10
- Medulla not interrupted type.....11
10. Scales strongly elongate.....*Gulo*
- Scales flattened.....12
11. Medulla absent or highly fragmental.....*Taxidea*
- Medulla continuous.....*Mephitis*
12. Cells of medulla separated by pigment masses.....*Canis*
- Cells of medulla not separated by pigment masses.....13
13. Distal portion of hair with cortical pigment.....*Mephitis*
- Distal portion of hair without cortical pigment.....14
14. Cells globular.....*Spilogale*
- Cells flattened.....15
15. Scale index at diam. 50 μ about 0.5.....*Thalarchos*
- Scale index at diam. 50 μ about 1.0.....*Alopex*
16. Pigment present.....17
- Pigment absent.....22
17. Medulla less than 0.3 of the shaft diameter.....18
- Medulla greater than 0.3 of the shaft diameter.....19
18. Medulla fragmentary.....*Conepatus*
- Medulla interrupted.....*Felis*
19. Medulla fragmentary, often highly so.....*Procyon*
- Medulla interrupted.....20
20. Cells separated by pigment masses.....21
- Cells not separated by pigment masses.....*Mustela*
21. Cortex lightly stained, yellowish.....*Felis*
- Cortex not stained.....*Lynx*
22. Medulla less than 0.3 of the shaft diameter.....23
- Medulla more than 0.3 of the shaft diameter.....26
23. Scales with broad distal line (see Fig. 65).....*Lutra*
- Scales not markedly elongate.....24
24. Medulla interrupted, pigment masses between cells.....*Canis*
- Medulla lacking pigment masses.....25
25. Medulla usually fragmental, scale index less than 0.7, pigment often present near tip.....*Mephitis*
- Medulla usually interrupted, scale index greater than 0.7.....*Taxidea*
26. Pigment masses between medullary cells.....27
- Pigment masses not present.....30

27. Scales strongly elongate, at least basal ones with distal tine.....*Martes*
Not so.....28
28. Scale index at 30 μ diameter under 1.00.....29
Scale index at 30 μ diameter over 1.00.....*Canis*
29. Medullary cells widely spaced.....*Bassariscus*
Medullary cells rather close together.....*Lynx*
30. Medulla interrupted.....31
Medulla fragmental, occasionally partly interrupted.....*Mephitis*
31. Scales flattened.....*Spilogale*
Scales elongate, at least slightly so.....32
32. Scale index at 25 μ over 1.00.....33
Scale index at 25 μ less than or just 1.00.....*Vulpes*
33. Scale index at 35 μ less than 0.9.....*Urocyon*
Scale index at 35 μ more than 0.9.....*Alopex*

As I have said in the introductory pages, these keys are not too trustworthy. The differences between the genera are real but in many instances defy generalization because so variable.

URSIDAE

THE BEARS

The protective hairs are long and usually between 100 and 200 micra in diameter at the widest part. The medulla rarely composes as much as 50 per cent of the shaft diameter, usually it is less than 40 per cent.

The fur hair is thick, coarse and kinky. The diameter ranges up to about 80 microns. The medulla is usually interrupted. There is a very scant deposit of medullary pigment in both *Euarctos* and *Ursus* and none in *Thalarchos*.

KEY TO THE GENERA OF *Ursidae*

Protective Hair

- 1 a. Medullary pigment absent.....*Thalarchos*
b. Medullary pigment present.....2
2 a. Average medulla less than 30 per cent of the shaft diameter.....*Ursus*
b. Average medulla greater than 30 per cent of the shaft diameter.....*Euarctos*

Fur Hair

- 1 a. Medullary pigment absent.....*Thalarchos*
b. Medullary pigment present.....2
2 a. Medulla "beaded," continuous.....*Euarctos*
b. Medulla usually absent or fragmental.....*Ursus*

EUARCTOS¹

The Black Bears

The hairs from the bears of this genus may be readily separated from those of *Ursus* upon the

¹In order to reduce the original manuscript to a more compact and more easily used form the descriptions of the hair as found in the various genera have been condensed to a mere outline of important characters. A uniform series of characters has been used to make comparison more simple and clear. Certain of these must be explained

proportionate diameter of the medulla of the protective hair.

PROTECTIVE HAIR

COLOR: white (rare): yellowish through the browns to black.

LENGTH: seldom exceeding 5 cm.

DIAMETER: 104 μ -190 μ ; mean 138 μ .

SCALE INDICES: basal 0.33 (110 μ), 0.40 (120 μ); mid-shaft 0.10 (170 μ).

CORTEX: stained and pigmented; reddish brown granules.

MEDULLA: index: 0.34 (0.186-0.425).

Form: continuous; thin plinths to almost globular cells.

Pigment: sparse, intercellular.

FUR HAIR

COLOR: white to dark brown.

LENGTH: 2 to 3 cm; kinky.

DIAMETER: 50 μ -76 μ ; mean 61 μ .

SCALES: usually prominent; index usually over 1.00, free margin fairly smooth and distally prolonged.

CORTEX: usually lightly stained and pigmented; unstained hairs do occur.

MEDULLA: index: 0.36 (0.31-0.50).

Form: interrupted, extreme basal usually fragmental; cells globular or cylindrical plinths.

Pigment: sparse; intercellular.

IMPORTANT CHARACTERISTICS

The structure of the medulla of the fur hair and the proportionate diameter of the medulla in the protective hairs are characteristics which serve to separate the bears of this genus from *Ursus*. The protective hair may be distinguished from the coarse hair from the back of the beaver, with which it might be confused under some conditions, by the very much greater scale index of the bear hair and the arrangement of the pigment granules in the cortex. The color and medullary proportion of the protective hair may lead to confusion of *Euarctos* with *Enhydra* from which separation is easy because of the peculiar abrupt distal swelling of the hair shaft in the latter genus.

in their abbreviated form. The Diameter given is that of the widest portion of the hair shaft as measured by means of an ocular micrometer. The Scale indices are accompanied by the diameter for the particular specimen noted. This figure is in parentheses. The index for the Medulla is the proportion of the shaft occupied by that structure at the widest part of the shaft.

The range and other specific data may be readily found in H. E. Anthony—*A Field-book of Mammals*, Putnam Co.

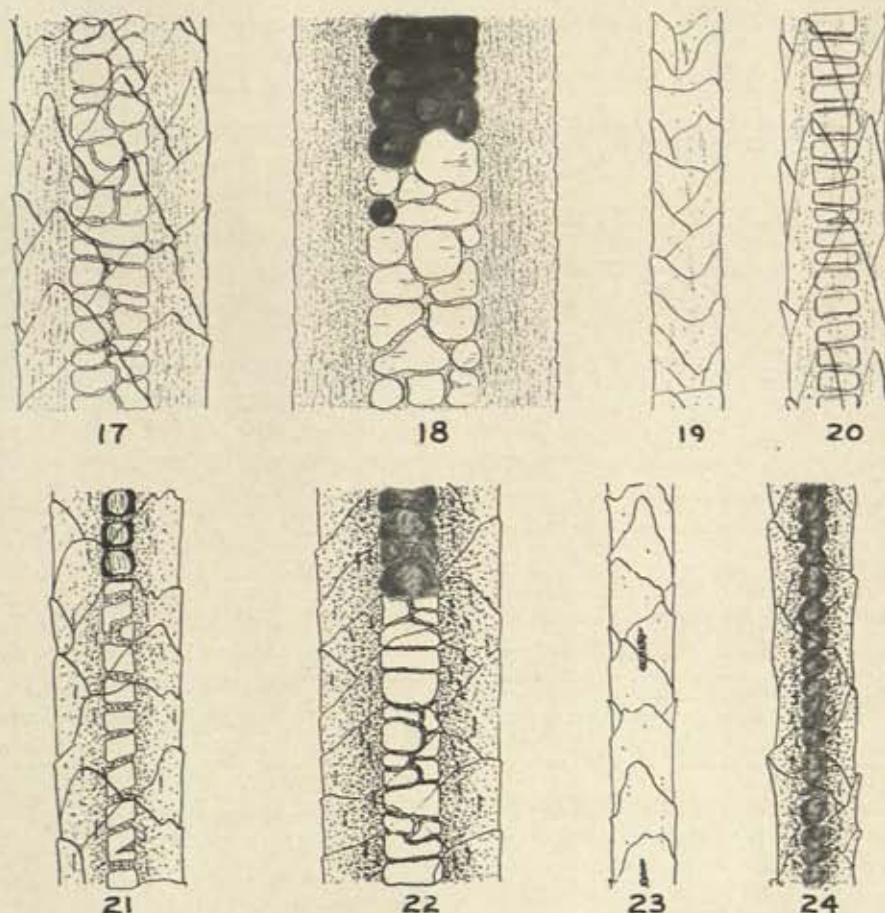
FIGS. 17 TO 24. *Euarctos americanus* (Pallas) CMNH 178.

FIG. 17.	protective	basal.	120 μ	FIG. 21.	protective	basal.	76 μ
FIG. 18.	protective	distad.	168 μ	FIG. 22.	protective	mid.	112 μ
FIG. 19.	fur	basal.	40 μ	FIG. 23.	fur	basal.	40 μ
FIG. 20.	fur	mid.	64 μ	FIG. 24.	fur	mid.	60 μ

URSUS

The Grizzly (and Big Brown Bears?)

The grizzly bears may be recognized immediately by the very slender medullary column. I have not had the opportunity to study the Big Brown Bears as yet but suspect that they too will show this characteristic.

PROTECTIVE HAIR

COLOR: usually rich brown; rarely whitish or black; frequently tipped with whitish in some species or races.

LENGTH: usually 6 to 8 cm rarely over 10 cm.

DIAMETER: 100 μ –260 μ ; mean 163 μ .

SCALE INDICES: basal 0.16 (176 μ); widest part 0.10 (248 μ).

CORTEX: usually deeply stained and lightly pigmented; color primarily due to stain.

MEDULLA: index: 0.27 (0.09–0.40).

Form: base—absent to fragmental. Mid-shaft—continuous, cells robust and of various rounded forms.

Pigment: rare; intercellular.

FUR HAIR

COLOR: dingy to blackish brown.

LENGTH: about 3 cm, curly.

DIAMETER: 44 μ –108 μ ; mean 77 μ .

SCALES: not very prominent; smoothly margined; index: 0.70 at the base to 0.50 in mid-section.

CORTEX: lightly stained and pigmented; color seems to be primarily due to pigment.

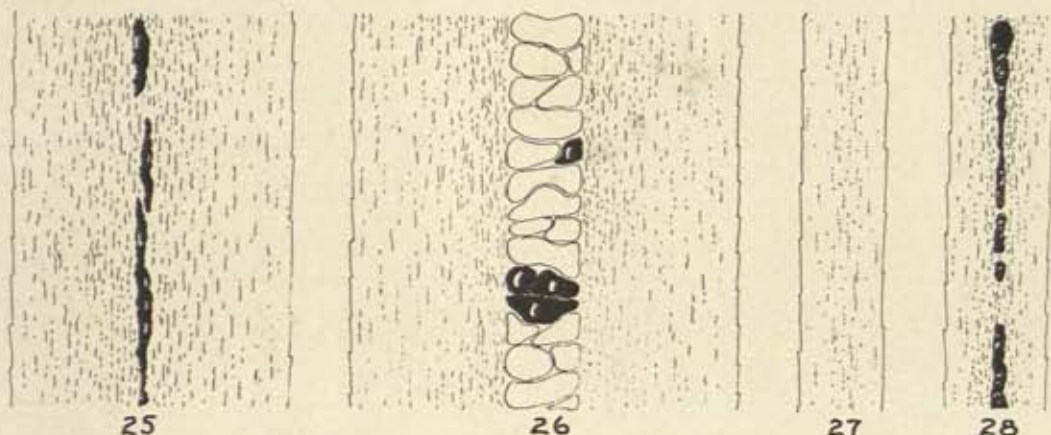
FIGS. 25 TO 28. *Ursus horribilis* Ord. CMZS.

FIG. 25. protective . . . basal 176 μ	FIG. 27. fur base 52 μ
FIG. 26. protective . . . mid 248 μ	FIG. 28. fur mid 64 μ

MEDULLA: index: 0.20 (0.12–0.27); absent in about 40 per cent of hairs examined.

Form: fragmental 90 per cent; continuous 10 per cent.

Pigment: absent.

IMPORTANT CHARACTERISTICS

The proportional diameter of the medulla plus uniformly great diameter seems to be diagnostic for *Ursus*.

THALARCTOS

Polar Bears

Nine out of ten times the hairs of these bears are easily identified. The total lack of pig-

mentation makes this so. The tenth time the confusion is that which might be brought about by the rare white hairs of the Kermode Bear (*Euarctos kermodei* (Hornaday)). White hairs from either *Ursus* or *Euarctos* usually have a scattering of very pale reddish brown pigment granules between the medullary cells.

PROTECTIVE HAIR

COLOR: white to yellowish.

LENGTH: usually not more than 3 cm.

DIAMETER: 80 μ –200 μ ; mean 139 μ .

SCALE INDICES: basal 0.16 (50 μ); mid-shaft 0.35 (128 μ); widest region 0.11 (160 μ).

CORTEX: rarely stained yellowish; no pigment; frequent fusi.

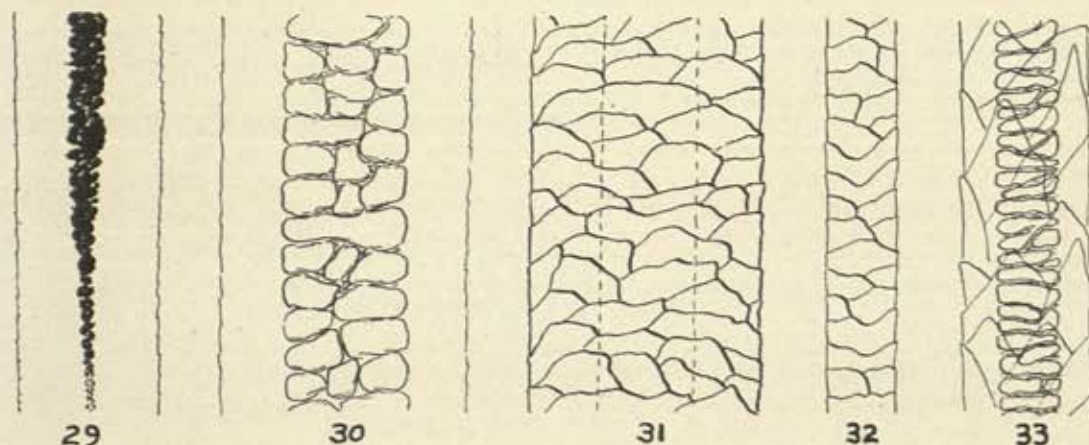
FIGS. 29 TO 33. *Thalarctos maritimus* (Phipps) CMNH 2708.

FIG. 29. protective . . . base 52 μ	FIG. 31. protective . . . mid 148 μ
FIG. 30. protective . . . mid 160 μ	FIG. 32. fur base 44 μ
FIG. 33. fur mid 80 μ	

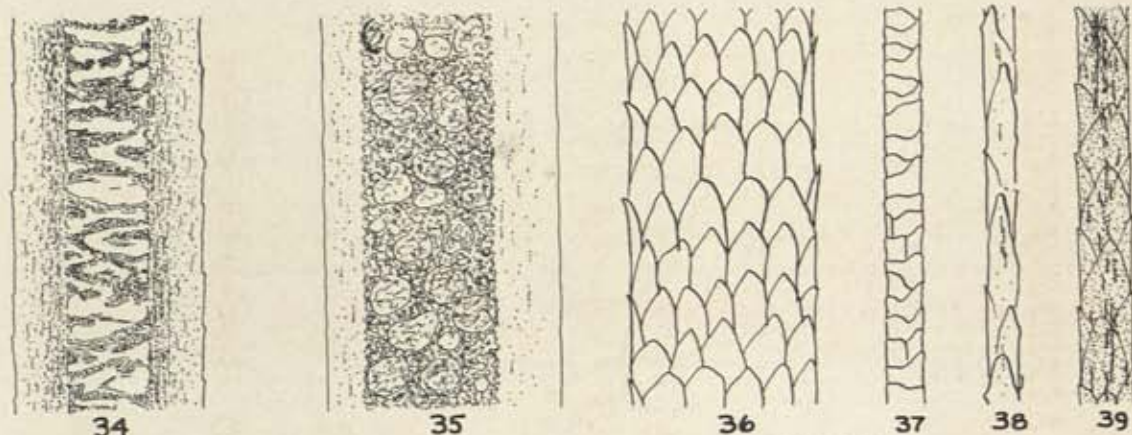
FIGS. 34 TO 39. *Procyon lotor lotor* (Linnaeus) CMNH 1855.

FIG. 34.	protective	basal.	120 μ	FIG. 37.	fur	base	24 μ
FIG. 35.	protective	mid.	152 μ	FIG. 38.	fur	basal.	20 μ
FIG. 36.	protective	basal.	120 μ	FIG. 39.	fur	mid.	34 μ

MEDULLA: *index*: 0.37 (0.19–0.50).

Form: continuous; flattened globular cells rather uniform in size.

Pigment: absent.

FUR HAIR

COLOR: white.

LENGTH: about 2 cm; kinky.

DIAMETER: 44 μ –120 μ ; mean 69 μ .

SCALES: fairly prominent; *indices*: basal 0.40 (44 μ), mid-shaft 0.80 (80 μ).

CORTEX: free of stain and pigment.

MEDULLA: *index*: 0.36 (0.25–0.50).

Form: continuous, the cells are thin plinths.

Pigment: absent.

IMPORTANT CHARACTERISTICS

The freedom from pigmentation and the relatively narrow medullary column should at once identify the hairs of *Thalarcos*.

PROCYONIDAE

PROCYON

Racoons

PROTECTIVE HAIR

COLOR: grey, brown, black and grizzled; white rare.

LENGTH: usually about 4 cm, occasionally to 6 cm.

DIAMETER: 100 μ –268 μ ; mean 161 μ .

SCALES: elongate, smooth margined, moderately prominent at the base; *indices*: basal 0.30 (120 μ), 0.10 (228 μ).

CORTEX: stained golden brown in pigmented areas; granules crowded toward medulla.

MEDULLA: *index*: 0.38 (0.19–0.53).

Form: continuous, cells variable in size and shape; impression is that medulla is a froth with various sized bubbles.

Pigment: considerable; intercellular.

FUR HAIR

COLOR: grey-white to deep brown.

LENGTH: 2–3 cm, kinky.

DIAMETER: 20 μ –60 μ ; mean 32 μ .

SCALES: prominent: basal region flat elsewhere elongate. *Indices*: basal 0.50 (30 μ); elsewhere 2.4 (20 μ), 1.6 (32 μ).

CORTEX: usually stained rich warm brown, stainless not rare; pigment granules well distributed, base usually free of pigment and stain.

MEDULLA: usually absent (90 per cent): highly fragmental in 10 per cent; in these the index averages 0.41 (0.33–0.67). *Pigment*: absent.

IMPORTANT CHARACTERISTICS

The medullary structure of the protective hairs is rather diagnostic *when considered for the whole length of the specimen*. This, plus non-medullated, well-pigmented fur hair with elongated scales should be considered almost positive.

BASSARISCIDAE

BASSARISCUS

Ring-tailed Cats

PROTECTIVE HAIR

COLOR: white, buff, grey and blackish brown; the darker hairs grizzled.

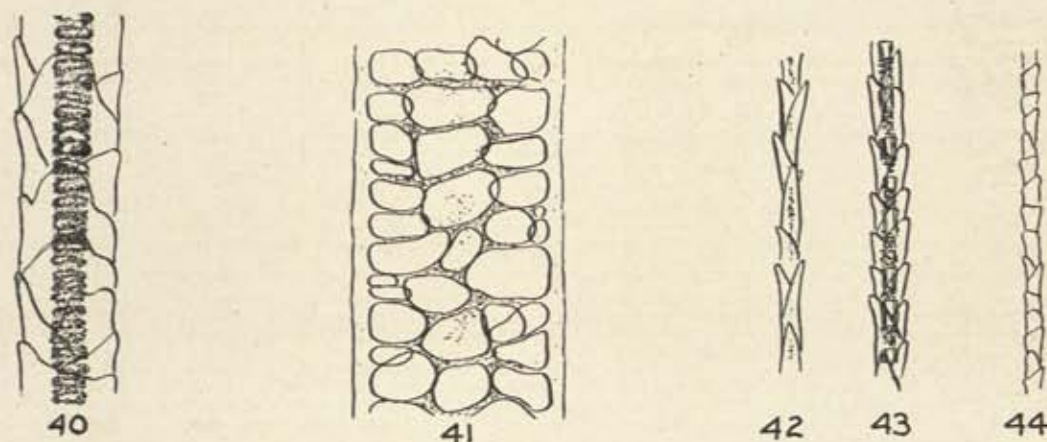
FIGS. 40 TO 44. *Bassaris astutus flavus* (Rhoads) CMNH 1990.

FIG. 40.....	protective... basal.....	60 μ	FIG. 42.....	fur..... base.....	12 μ
FIG. 41.....	protective... mid.....	136 μ	FIG. 43.....	fur..... mid.....	20 μ
FIG. 44.....	fur..... tip.....	10 μ			

LENGTH: usually less than 2 cm, rarely over 3 cm.

DIAMETER: 95 μ –150 μ ; mean 107 μ . Back hairs consistently coarser than flank or belly hairs.

SCALES: smoothly rounded, prominent at base; indices: basal, 0.8 (64 μ); widest part, 0.16? (100 μ).

CORTEX: faintly stained yellow-brown in dark areas; dark brown pigment granules.

MEDULLA: index: 0.77 (0.60–0.84).

Form: continuous, semi-globular cells.

Pigment: abundant, intercellular, light reddish brown granules.

FUR HAIR

COLOR: white or greyish.

LENGTH: about 1.5 cm, rarely 2 cm.

DIAMETER: 20 μ –30 μ ; mean 23.6 μ .

SCALES: prominent; basal and those in narrow parts of shaft strongly produced, smooth-edged and flaring, in widest parts appressed and not produced distally. Index: 1.8 (20 μ) to 0.53 (28 μ).

CORTEX: free of stain and pigment.

MEDULLA: index: 0.55 (0.37–0.67).

Form: fragmental at base, elsewhere interrupted, cells widely spaced cylindrical plinths.

Pigment: small clusters of faintly colored granules attached to basal surface of the cells.

IMPORTANT CHARACTERISTICS

The shape of the medullary cells in the basal portion of the protective hair plus the character-

istic of the diameter and large proportion of medulla will help to set this genus apart from those with which it may be confused. The diameter, scale form, and medullary pigment, when taken together, will identify the fur hair.

MUSTELIDAE

WEASELS, SKUNKS, BADGERS, etc.

Nine genera of the *Mustelidae* are found in North America. These are divided among six sub-families. I have been unable to detect any character or combination of characters that will set this family apart from other *Carnivora*. Many of the members are important fur-bearers today and doubtlessly were to the aborigines as well. I have seen strands of wool made from *Lutra* fur and have seen many pieces of clothing and adornment incorporating the furry hides of these animals. A beautiful Blackfoot headdress (FBI-45-P, Denver Art Museum Coll.) is made almost wholly of the tails of *Mustela longicauda*. A Nez Perce shirt belonging to William Berger, Jr. in Denver is trimmed with fur from *Enhydra*.

MUSTELINAE

MARTENS, WEASELS AND MINK

Martes and *Mustela* represent this sub-family in the territory covered by this paper. Relatively short carnivore hairs (under 3 cm) with the medulla composing over 50 per cent of the shaft in the basal region and made up of flattened cells extending across the full column may with fair reliability be assigned to this sub-family.

KEY TO THE PROTECTIVE HAIRS

- 1 a. Medullary cells at the base robust, flattened, often two joined together as in horizontal "U" or "H"..... *Martes*
 b. Medulla at the base without distinct cells but deeply indented giving the impression of flattened cells..... *Mustela*

KEY TO FUR HAIRS

- 1 a. Cuticular scales at the base with a long slender tine pointing distad..... *Martes*
 b. Cuticular scales lacking these tines..... *Mustela*

MARTES

Martens and Fishers

PROTECTIVE HAIR

COLOR: from white to black; usually some shade of brown.

LENGTH: from 2.5 to 4 cm, occasionally 5 cm.

DIAMETER: 72 μ –176 μ ; mean 136 μ .

SCALES: prominent in basal portion, acuminate; rather inconspicuous elsewhere; index: 1.1 (72 μ) basal; 0.10 (150 μ).

CORTEX: lightly stained; very small, rich brown granules abundant.

MEDULLA: index: 0.67 (0.60–0.79).

Form: continuous; cells robust, some joined in simple shapes as horizontal "U's" and "H's" in basal area.

Pigment: fine, intercellular granules.

FUR HAIR

COLOR: pale greyish brown to white.

LENGTH: about 2 cm.

DIAMETER: 20 μ –36 μ ; mean 28 μ .

SCALES: the cuticular scales at the base are interesting in that they bear a long slender digitate tine on the distal margin. This is almost equal to the free proximo-distal dimension in length. A similar process is found in *Lutra*. In that genus the base of the process is tapered; in this the tine is an abrupt projection from the free margin. The scales of the body of the hair are acuminate and in that way differ from the scales in the same region of the fur hair of *Lutra* where they are similar to those of the base but broadened. The scales at the tip are simple and flattened. Index: basal about 5.0 (diam. 20 μ); wider parts 1.7 (diam. 30 μ).

CORTEX: occasionally lightly stained.

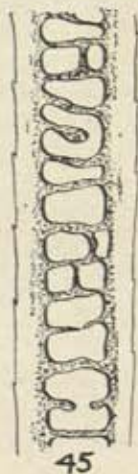
MEDULLA: index: 0.56 (0.43–0.67).

Form: interrupted.

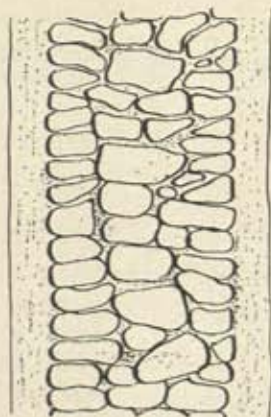
Pigment: doubtfully present between the cells.

IMPORTANT CHARACTERISTICS

The form of the medulla plus the acuminate scales at the base is a fairly reliable combination of characteristics for the protective hairs. The cuticular scales and their variation in shape is a reliable basis for the identification of the fur hair.



45



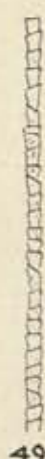
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47



48



49

FIGS. 45 TO 49. *Martes caurina* (Merriam) CMNH 48.

FIG. 45.....	protective.....	basal.....	78 μ	FIG. 47.....	fur.....	base.....	14 μ
FIG. 46.....	protective.....	distal.....	172 μ	FIG. 48.....	fur.....	mid.....	32 μ
FIG. 49.....	fur.....	tip.....	8 μ				

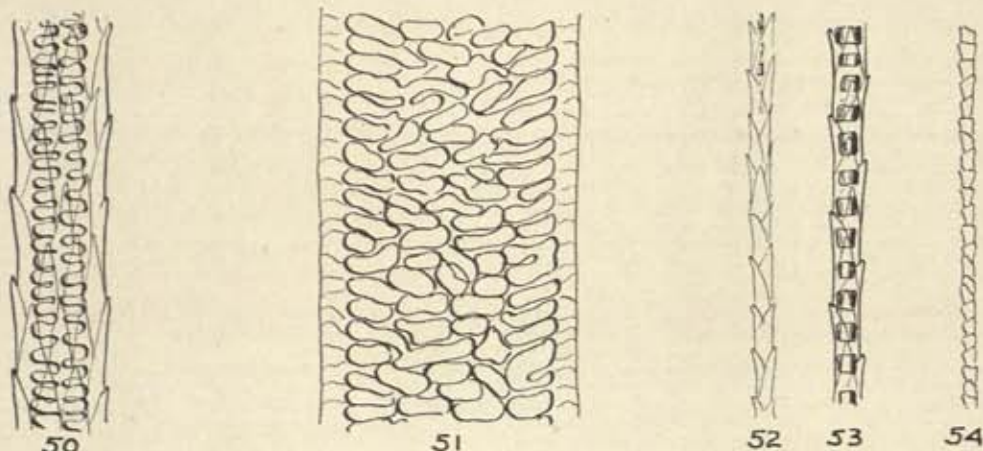
FIGS. 50 TO 54. *Mustela arizonensis* (Mearns) CMNH 1557.

FIG. 50.....	protective...basal.....	60 μ	FIG. 52.....	fur.....base.....	12 μ
FIG. 51.....	protective...distal.....	168 μ	FIG. 53.....	fur.....mid.....	22 μ
FIG. 54.....	fur.....tip.....	8 μ			

MUSTELA

Weasels and Mink

PROTECTIVE HAIR

COLOR: white, yellowish, black and all varieties of brown.

LENGTH: seldom exceeding 2 cm for weasels, a little longer in mink.

DIAMETER: 92 μ –176 μ ; mean 149 μ . Hairs of the flank on the average show less distal swelling than do the hairs from the back. A five-fold increase in diameter is not uncommon.

SCALES: prominent in the basal region; basal acuminate, elsewhere flattened. *Index*: basal 1.60 (48 μ), 0.84 (60 μ); elsewhere 0.12 (140 μ), 0.07 (168 μ).

CORTEX: white—free of stain and pigment. Yellowish—stained with little pigment. Brown—stained and pigmented, granules small and scattered.

MEDULLA: *index*: 0.80 (0.56–0.87).

Form: continuous, characteristic at base, see figure 50.

Pigment: absent.

FUR HAIR

COLOR: pale to white.

LENGTH: about 1.5 cm.

DIAMETER: 15 μ –30 μ ; mean 22 μ .

SCALES: acuminate at base, flattened elsewhere.

CORTEX: as in protective hair but never so intensely.

MEDULLA: *index*: 0.66 (0.50–0.75).

Form: interrupted.

Pigment: absent.

IMPORTANT CHARACTERISTICS

The cells of the medulla of the protective hair present a reliable index to this genus. The fur hair is less easily recognized but the scale index and form taken with the diameter is fairly reliable.

GULONINAE

GULO

Wolverines

The wolverines are the largest of the weasel family. They are found over the northern part of the continent southward to the northernmost states of the United States and through the Rockies as far south as Colorado.

PROTECTIVE HAIR

COLOR: grizzled, light at base, yellowish to dark brown at tip.

LENGTH: up to 10 cm.

DIAMETER: 160 μ –264 μ ; mean 204 μ . Those of the back 160 μ –192 μ .

SCALES: the cuticular scales at the extreme base are flattened and the free margin is rough. As the medulla becomes continuous the scales elongate and become acuminate with smooth margins. As the full width of the hair is approached these scales again change form to a flattened, smooth-margined type. The scale index at the extreme base,

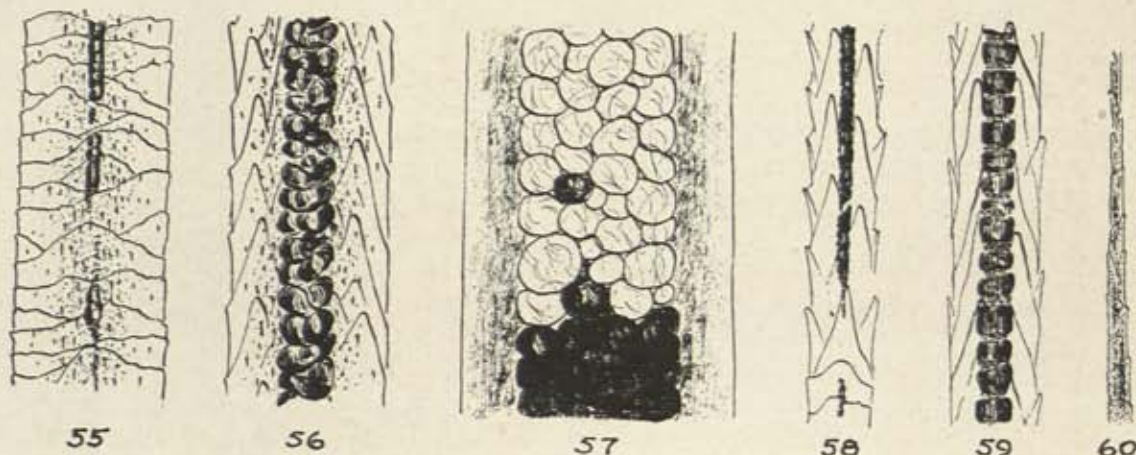
FIGS. 55 TO 60. *Gulo luscus* (Linnaeus) CMNH 1949.

FIG. 55.....	protective.....basal.....	96 μ	FIG. 58.....	fur.....base.....	40 μ
FIG. 56.....	protective.....basal.....	100 μ	FIG. 59.....	fur.....mid.....	56 μ
FIG. 57.....	protective.....mid.....	176 μ	FIG. 60.....	fur.....tip.....	8 μ -16 μ

where the medulla is narrow and fragmentary, is 0.12 (diam. 96 μ). In the region of acuminate scales it is 0.40 (diam. 96 μ) and at the widest part of the hair 0.08 (diam. 176 μ).

CORTEX: stain and pigment vary with color of hair; fusi prominent and appear like elongate pigment granules.

MEDULLA: index: 0.52 (0.41-0.64), from back 0.54-0.64.

Form: continuous, except for extreme base and tip, these fragmentary, cells globose.

Pigment: present?

FUR HAIR

COLOR: light.

LENGTH: 3 to 4 cm, kinky.

DIAMETER: 40 μ -76 μ ; mean 50 μ .

SCALES: acuminate except base and tip, then flattened; index: non-medullated base 0.39 (32 μ), medullated base 1.30 (35 μ), elsewhere 0.46 (64 μ).

CORTEX: usually free of stain, pigment rare except in distal portion when it seems to be the rule.

MEDULLA: index: 0.45 (0.32-0.54).

Form: interrupted.

Pigment: scant, intercellular.

IMPORTANT CHARACTERISTICS

The globular cells of the medulla plus the gradual development of the medulla at the base and the changes in the form of the scales throughout the length of the hair shaft seem to charac-

terize the protective hair of the wolverine. The fur hair may be recognized by its coarseness and the shape of the scales.

LUTRINAE

LUTRA

Otters

PROTECTIVE HAIR

COLOR: shades of brown.

LENGTH: up to 3 cm, rarely 6 cm.

DIAMETER: 235 μ -330 μ ; mean 280 μ . The distal portion of the hairs is usually markedly wider than the proximal (Fig. 3). In some instances this increase may exceed by six-fold the narrowest portion of the hair. Most of the hairs have a curious reduction in the diameter about a quarter of the length of the hair from the base. This may amount to as much as 50 per cent and occurs in the short space of a hundred or so microns. The swollen portion of the shaft seldom occupies more than the distal third of the hair. It tapers abruptly to the tip.

SCALES: flattened at the base, acuminate through the distal two-thirds and flattened in the swollen portion. **Indices:** extreme base 0.16 (80 μ), beginning of medulla 0.43 (104 μ), just basad of constriction 0.83 (96 μ), just distad of constriction 1.00 (64 μ), widest part 0.12 (304 μ).

CORTEX: stained yellowish brown and well filled with pigment granules. Throughout most of the densely colored parts of the

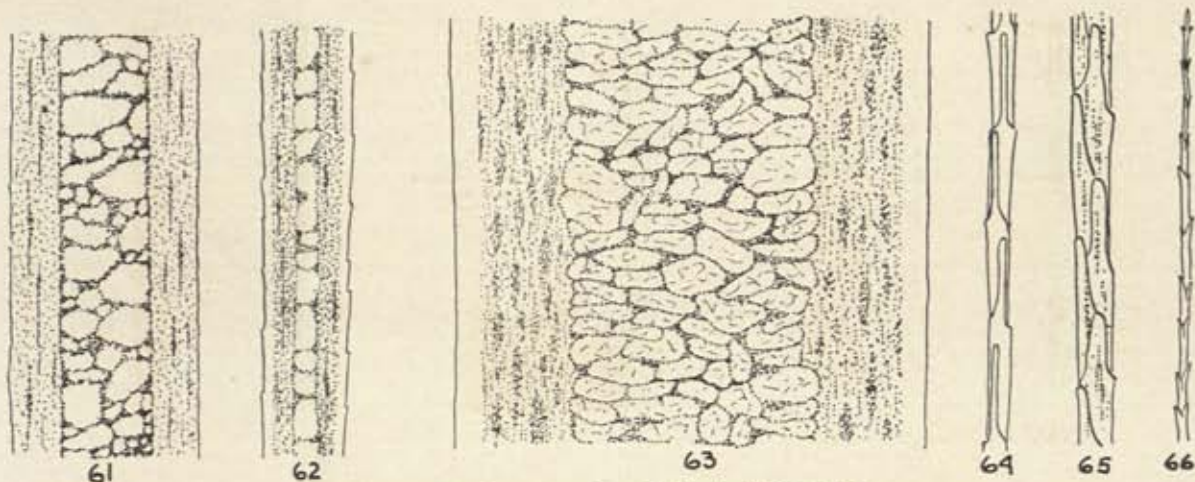
FIGS. 61 TO 66. *Lutra canadensis* (Schreber) CMNH 92.

FIG. 61	protective	base	120 μ
FIG. 62	protective	basad	56 μ
FIG. 63	protective	distal	308 μ

FIG. 64	fur	base	20 μ
FIG. 65	fur	mid	24 μ
FIG. 66	fur	tip	6 μ

shaft there is a narrow margin of cortical (possibly cuticular) material free of stain and pigment.

MEDULLA: index: 0.53 (0.34–0.60).

Form: continuous, large cells with interstices filled with small ones.

Pigment: some intercellular granules.

FUR HAIR

COLOR: colorless, rarely brownish.

LENGTH: 1.0–1.5 cm, curly to kinky.

DIAMETER: 12 μ –24 μ ; mean 16 μ .

SCALES: the cuticular scales are widely spaced, having an index ranging between 4.0 and 6.0.

They are distinctive in form, there being a long digitate tine on the free margin. This tine is very narrow in the basal portion of the hair and broader in the distal portion.

CORTEX: usually free of pigment and stain.

MEDULLA: usually absent: when present (5 per cent) highly fragmental and accompanied by light distal pigmentation of the cortex.

IMPORTANT CHARACTERISTICS

The peculiar shape of the longitudinal section of the protective hair is characteristic of *Lutra*. When this is absent the small flattened medullary cells and the full medullation of the extreme base will serve to indicate the genus. The fur hair may be recognized by the form of the scales. The considerable medulla in the protective hair and the general lack of pigment in the fur hair will serve to separate this genus from the following, *Enhydra*.

ENHYDRINAE

ENHYDRA

Sea Otters

PROTECTIVE HAIR

COLOR: dark brown, lighter toward the base.

LENGTH: 2–3 cm.

DIAMETER: 64 μ –200 μ ; mean 120 μ .

SCALES: smooth-margined, produced except in widest part of shaft, then flattened. Indices: base 0.88 (92 μ), mid-region 0.24 (168 μ), widest part 0.06 (200 μ).

CORTEX: lightly stained, pigmentation in basal half light and in distal half very dense, granules small.

MEDULLA: index: impossible to measure due to density of cortical pigment in most hairs. Less than 0.20 in those measured.

Form: fragmentary to continuous, generally absent in flank hairs.

Pigment: probably absent.

FUR HAIR

COLOR: dingy brown, much lighter toward the base.

LENGTH: 1–1.5 cm.

DIAMETER: 20 μ –56 μ ; mean 31 μ .

SCALES: very much like those of *Lutra* q.v.

Indices: 4.0 (20 μ), 2.0 (24 μ), 1.8 (36 μ).

CORTEX: faintly stained, pigmentation variable, from densely packed dark brown to scattered pale brown granules.

MEDULLA: rarely present, then fragmentary 0.20–0.60.

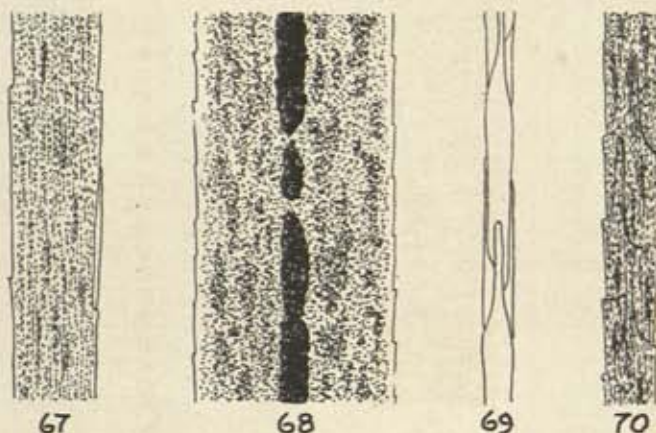
FIGS. 67 TO 70. *Enhydra lutris* (Linnaeus) AMNH 75333.

FIG. 67	protective	basal	58 μ	FIG. 69	fur	base	16 μ
FIG. 68	protective	mid	128 μ	FIG. 70	fur	mid	32 μ

IMPORTANT CHARACTERISTICS

The very slender medullary column of the protective hairs may lead to confusion with Bears or Raccoon. The typical abrupt swelling of the distal portion of the hair will serve to separate *Enhydra* from these. The swelling may confuse the hairs from this genus with those of *Lutra*. The hairs of *Enhydra* are easily separated by the very narrow medullary column they contain.

The fur hairs are difficult to separate with absolute certainty from those of *Lutra*. In general the fur hairs of *Lutra* lack pigment granules while those of *Enhydra* contain them.

b. Clear, hyaline margin rare in dark hairs; few of the cells in the medulla of white hairs flattened.

Mephitis
Note.—*Mephitis* and *Conepatus* do not always separate according to the key for protective hairs.

Fur Hair

- 1 a. Medulla in central portion of the shaft interrupted. *Spilogale*
- b. Medulla in the central portion of the shaft continuous or fragmentary. 2
- 2 a. Medulla fragmentary. *Conepatus*
- b. Medulla continuous or interrupted. *Mephitis*

Note.—*Spilogale* and *Mephitis* do not always separate according to the key for fur hairs.

Note.—*Conepatus* may always be recognized by its very low scale index.

SPILOGALE

The Spotted Skunks

PROTECTIVE HAIR

COLOR: white—or black with whitish base.

LENGTH: up to 4 cm.

DIAMETER: 40 μ –204 μ ; mean 111 μ .

SCALES: flattened—crenate margins; indices: basal 2.4 (24 μ), mid-region 0.35 (52 μ), widest part 0.12 (84 μ).

CORTEX: white—free of stain and pigment.

Black—strongly stained, large dark granules.

MEDULLA: index: 0.62 (0.31–0.79).

Form: continuous, occasionally interrupted, cells at base globular and those in wide regions strongly flattened and often linked together into irregular flattened forms.

Pigment: sparse to absent.

FUR HAIR

COLOR: usually colorless.

LENGTH: under 2 cm.

MEPHITINAE

SKUNKS

The skunks are found over the entire North American continent from 50° N southward. They range farther north than this in the west. The family is well represented by three genera, *Spilogale*, *Mephitis*, and *Conepatus*. The genera are separable one from the others on the basis of hair structure but as yet I have been unable to find a set of characters that will isolate the family.

A KEY TO THE HAIR OF THE *Mephitinae*

Protective Hair

- 1 a. Medulla at the extreme base continuous, cells globular, in the mid-section continuous, cells flattened and often linked. *Spilogale*
- b. Medulla at base fragmentary. 2
- 2 a. Dark portion of the hair with a clear, hyaline margin; white hairs with the majority of the medullary cells flattened but not linked. *Conepatus*

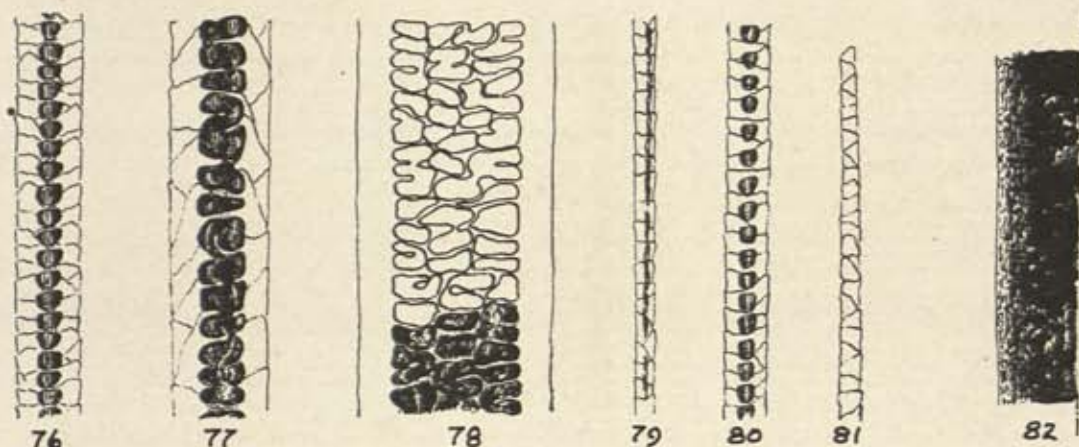
FIGS. 76 TO 82. *Spilogale a. arizonae* (Mearns) ERW 3366.

FIG. 76.....	protective...basal.....	40 μ	FIG. 79.....	fur.....base.....	12 μ
FIG. 77.....	protective...basal.....	60 μ	FIG. 80.....	fur.....mid.....	28 μ
FIG. 78.....	protective...mid.....	124 μ	FIG. 81.....	fur.....tip.....	10 μ
FIG. 82.....	protective...mid.....	pigmented			

DIAMETER: 16 μ –56 μ ; mean 26 μ .

SCALES: smooth and flattened. *Indices*: basal 1.8 (12 μ), mid-section 1.5 (20 μ) and 0.95 (28 μ).

CORTEX: usually free of pigment and stain.

MEDULLA: *index*: 0.41 (0.33–0.67).

-*Form*: interrupted.

Pigment: absent.

IMPORTANT CHARACTERISTICS

The arrangement and form of the cells in the mid-shaft medulla of the protective hairs and

the interrupted medullary column of the fur hairs are good characteristics.

MEPHITIS

The Striped Skunks

PROTECTIVE HAIR

COLOR: same as *Spilogale* q.v.

LENGTH: up to 7 cm.

DIAMETER: 48 μ –248 μ ; mean 150 μ .

SCALES: flattened with crenate margin except at base when they are produced. *Indices*:

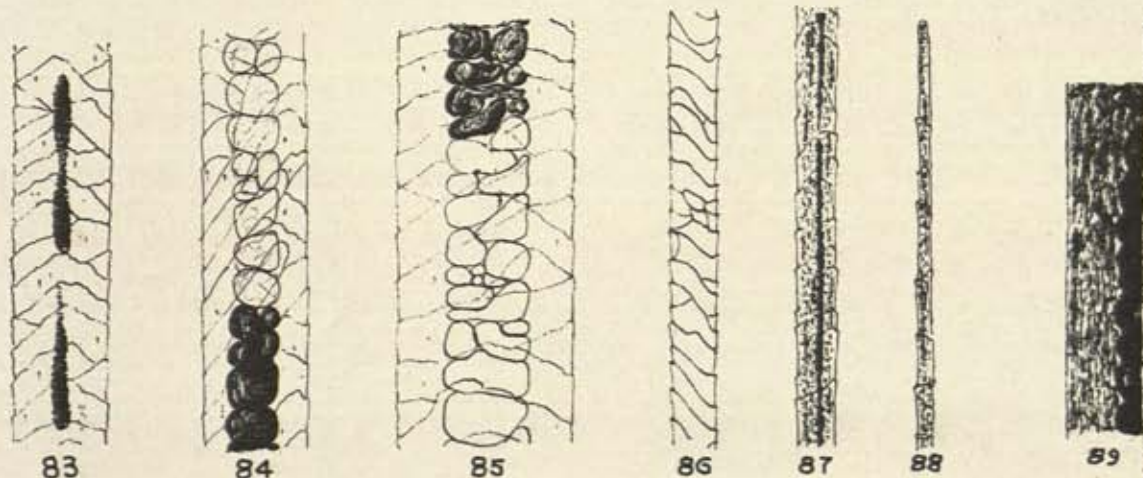
FIGS. 83 TO 89. *Mephitis hudsonica* (Richardson) ERW 1351.

FIG. 83.....	protective...basal.....	60 μ	FIG. 86.....	fur.....base.....	28 μ
FIG. 84.....	protective...basal.....	64 μ	FIG. 87.....	fur.....distal.....	24 μ
FIG. 85.....	protective...mid.....	112 μ	FIG. 88.....	fur.....tip.....	8 μ
FIG. 89.....	protective...mid.....	pigmented			

base 0.21 (74 μ), medullate base 0.14 (104 μ), mid-section 0.07 (176 μ).

CORTEX: white—free of pigment and stain. Black: as in *Spilogale* but with smaller granules.

MEDULLA: index: 0.52 (0.32–0.80).

Form: continuous—more or less globular cells a few of which are compressed or distorted.

Pigment: absent.

FUR HAIR

COLOR: dusky.

LENGTH: 2–3 cm, wavy.

DIAMETER: 24 μ –64 μ ; mean 37 μ .

SCALES: smooth and flattened. Indices: at base 0.52 (32 μ), medullated base 0.66 (32 μ), widest part 0.40 (56 μ), tip 1.25 (16 μ).

CORTEX: usually free of stain except at tip, pigmentation most dense in wide parts of the hair.

MEDULLA: index: 0.30 (0.14–0.50).

Form: usually continuous, rarely pigmented or interrupted in the mid-section.

Pigment: absent.

IMPORTANT CHARACTERISTICS

The continuous nature of the medulla of the fur hair coupled with its diameter will serve to separate *Mephitis* and *Conepatus*. The medulla of the protective hair is constant in its difference from that of *Spilogale*. The clear cuticular region of *Conepatus* will separate the protective hair of that genus from this. The color of the hair is sufficient to differentiate *Mephitis* from *Felis*.

CONEPATUS

The Hog-nosed Skunks

PROTECTIVE HAIR

COLOR: dorsum, white; belly, dusky brown; flanks, black lighter at base.

LENGTH: 4–7 cm.

DIAMETER: 84 μ –300 μ ; mean 189 μ .

SCALES: flattened, crenate margin. Indices: basal 0.15 (92 μ), widest part 0.06 (180 μ).

CORTEX: about as in *Mephitis* q.v.

MEDULLA: index: 0.53 (0.34–0.66).

Form: continuous except at base, then fragmentary, cells flattened.

Pigment: intercellular, always present, even in white hairs.

FUR HAIR

COLOR: dusky to dark brown.

LENGTH: about 2.5 cm.

DIAMETER: 28 μ –80 μ ; mean 46 μ .

SCALES: flattened. Indices: from very fine hair, base 0.51 (28 μ), wide portion 0.55 (40 μ); from coarse hair 0.32 (48 μ), 0.19 (60 μ).

CORTEX: always pigmented and often stained lightly especially toward tip.

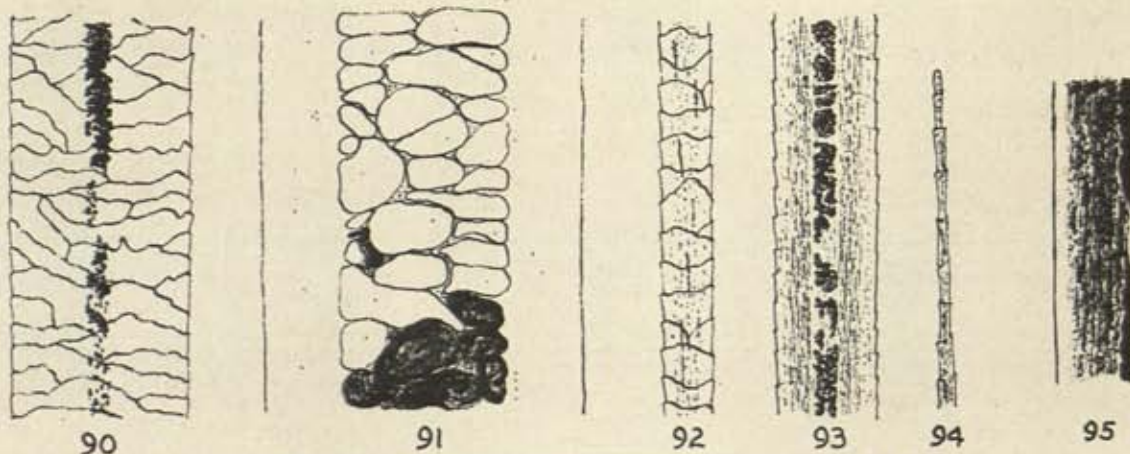
MEDULLA: index: 0.21 (0.00–0.25).

Form: absent or fragmentary.

Pigment: irregular intercellular masses.

IMPORTANT CHARACTERISTICS

The large, irregular, flattened cells of the medulla of the protective hair plus the distinctly colorless cuticular zone will serve to identify this genus from those with which it might be confused. The medulla offers a good key to the fur hair.



FIGS. 90 TO 95. *Conepatus mesoleucas mearnsi* (Merriam) ERW 4252.

FIG. 90. protective . . . basal 108 μ
FIG. 91. protective . . . mid 208 μ
FIG. 92. fur base 32 μ

FIG. 93. fur mid 64 μ
FIG. 94. fur tip 10 μ
FIG. 95. protective . . . mid pigmented

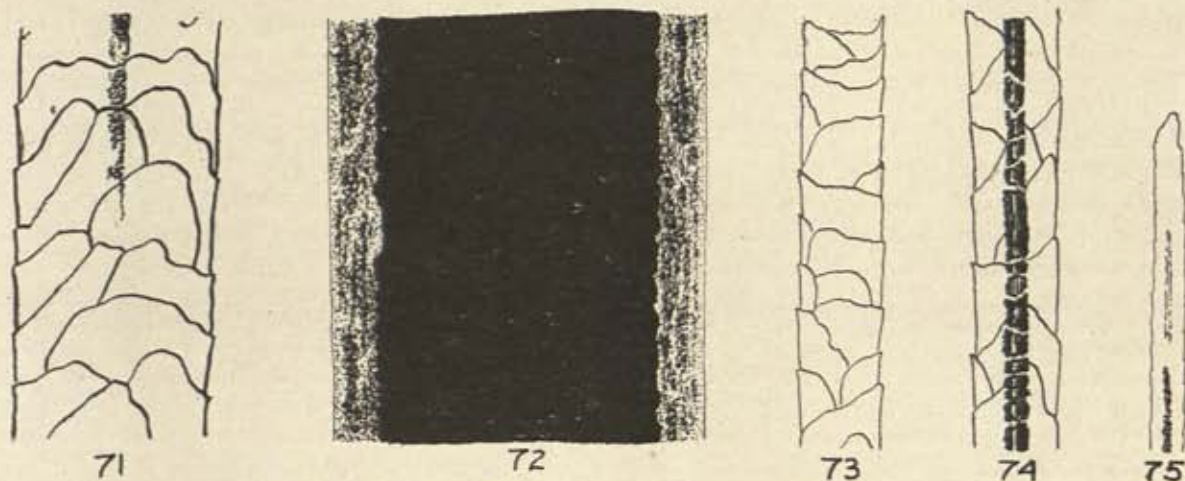
FIGS. 71 TO 75. *Taxidea taxus taxus* (Schreber) ERW 95.

FIG. 71.....	protective..	basal.....	124 μ	FIG. 73.....	fur.....	base.....	52 μ
FIG. 72.....	protective..	mid.....	240 μ	FIG. 74.....	fur.....	mid.....	52 μ
FIG. 75.....	fur.....	tip.....	20 μ				

TAXIDIINAE

TAXIDEA

Badgers

PROTECTIVE HAIR

COLOR: grizzled, light at tip and base.

LENGTH: about 6-8 cm.

DIAMETER: 160 μ -300 μ ; mean 222 μ .

SCALES: irregular margins, prominent at the base. *Indices*: basal 0.16 (120 μ), medullated base 0.30 (120 μ), mid-section 0.28 (144 μ), widest portion 0.09 (264 μ).

CORTEX: free of stain in lightest parts, dark parts stained and filled with rather large ovoid reddish granules often gathered in flocculent groups.

MEDULLA: *index*: 0.75 (0.52-0.91); in basal region about 0.25 and gradually increasing to about 0.80.

Form: continuous, small compact cells.

Pigment: absent.?

FUR HAIR

COLOR: colorless or dingy grey.

LENGTH: 2-3 cm.

DIAMETER: 36 μ -60 μ ; mean 48 μ .

SCALES: prominent, slightly irregular margins.

CORTEX: free of pigment and stain.

MEDULLA: *index*: 0.30 (0.27-0.47).

Form: absent in the base, otherwise a continuous column of flattened globose cells.

Pigment: scattered pale intercellular granules.

IMPORTANT CHARACTERISTICS

The gross aspects of the hair combined with the scale form and the diameters of the medullary column throughout the shaft are safe characters for the identification of *Taxidea*.

CANIDAE

The four genera of the canines that are found in North America are grouped together in the sub-family *Caninae*. The scales of the protective hairs and the character of the medulla in the wide part of the shaft are fair characters for separating these mammals from the other carnivores found in the range covered by this paper. In the *Caninae* the scales on the shaft in its widest part are generally elongate.

CANINAE

The genera are easily separated by an examination of the whole shaft under the microscope.

KEY TO THE GENERA

Protective Hair

- 1 a. Scale index at middle part of the hair greater than 0.3..... *Urocyon*
- b. This index less than 0.3..... 2
- 2 a. Seldom more than two "courses" of cells across the medulla..... *Vulpes*
- b. Seldom less than four "courses" of cells across the medulla in the widest part of the shaft..... 3
- 3 a. Medulla about 60 per cent of the shaft diameter at its widest part..... *Alopex*
- b. Medulla more than 75 per cent of the shaft diameter at its widest part..... *Canis*

Fur Hair

- 1 a. Pockets of pigment between the medullary cells.....*Canis*
b. These pigment pockets lacking.....2
- 2 a. Scales strongly elongate at the base of the hair.....3
b. Scales not strongly elongate at the base of the hair.....*Vulpes*
- 3 a. Medulla usually more than 50 per cent of the diameter of the shaft at its widest part.....*Alopex*
b. Medulla seldom approaching 50 per cent of the diameter of the shaft at its widest part.....*Urocyon*

Note.—Bracket three in the above breaks down too frequently to be of much use, but the rarity of *Alopex* and its range will often eliminate that genus.

VULPES

The Red Foxes

PROTECTIVE HAIR

COLOR: usually rusty red to buff, occasionally black, brown, grizzled or white.

LENGTH: up to 8 cm.

DIAMETER: 108 μ –220 μ ; mean 153 μ .

SCALES: difficult to see; slightly elongate, crenate margins, basal scales strongly produced. *Indices*: base 0.17 (120 μ), basal 0.28 (116 μ), mid-section 0.19 (104 μ); widest part 0.10 (152 μ).

CORTEX: lightly stained yellow; pigment granules are small and vary in quantity and color, light reddish brown to rich brown.

MEDULLA: *index*: 0.74 (0.60–0.84).

Form: the medulla is composed of rather uniform sized cells of modified globular shape with occasional large flat cells. In the widest part of the shaft the medulla

frequently takes on an entirely different aspect. In these instances the majority of the cells are so compressed as to appear like thin wafers across the medulla. In this a few of the cells retain their more or less globular form. This is the usual type of medulla in the genus *Lynx* where the non-flattened cells are very large. These globose cells in *Vulpes* are generally small and seldom exceed one-third of the medullary diameter in their greatest dimension.

Pigment: intercellular.

FUR HAIR

COLOR: colorless or yellowish.

LENGTH: about 2 cm, kinky.

DIAMETER: 20 μ –40 μ ; mean 26 μ .

SCALES: prominent, smooth margined.

Index: 1.0 (24 μ).

CORTEX: free of pigment, usually free of stain.

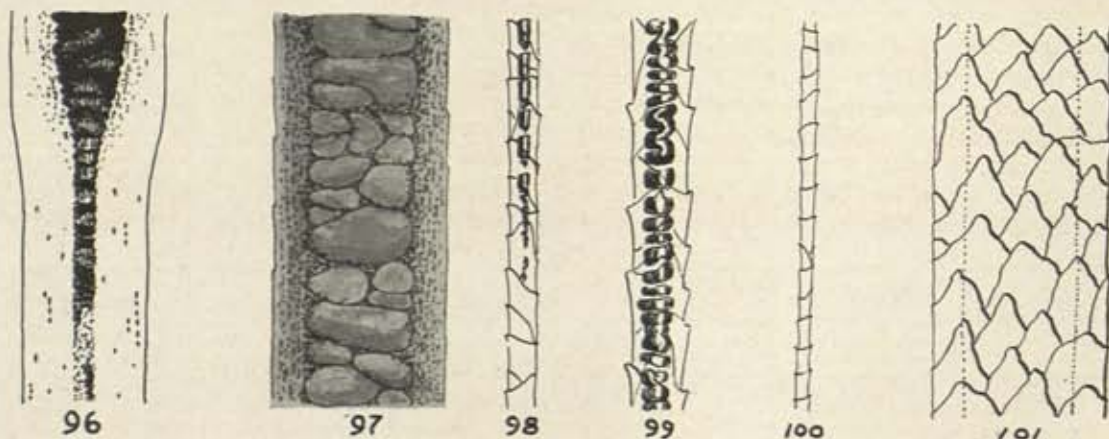
MEDULLA: *index*: 0.70 (0.60–0.80).

Form: continuous column of cylindrical plinths.

Pigment: absent.

IMPORTANT CHARACTERISTICS

The color of the pigment granules is rarely met in hairs with which these might be confused. In the case of *Lynx* the size of the inflated cells in the medulla at the widest part of the shaft will give the cue. They are much smaller in *Vulpes*. From *Urocyon* the dark hairs may be separated by the prominence of the cuticular



FIGS. 96 TO 101. *Vulpes velox velox* (Say) ERW 4367.

FIG. 96.....protective...base.....80 μ –100 μ

FIG. 97 pigmentation reduced for clarity.....protective...mid.....108 μ

FIG. 98.....fur.....base.....16 μ

FIG. 99.....fur.....mid.....40 μ

FIG. 100.....fur.....tip.....9 μ

FIG. 101 detail of scales.....protective...mid.....112 μ

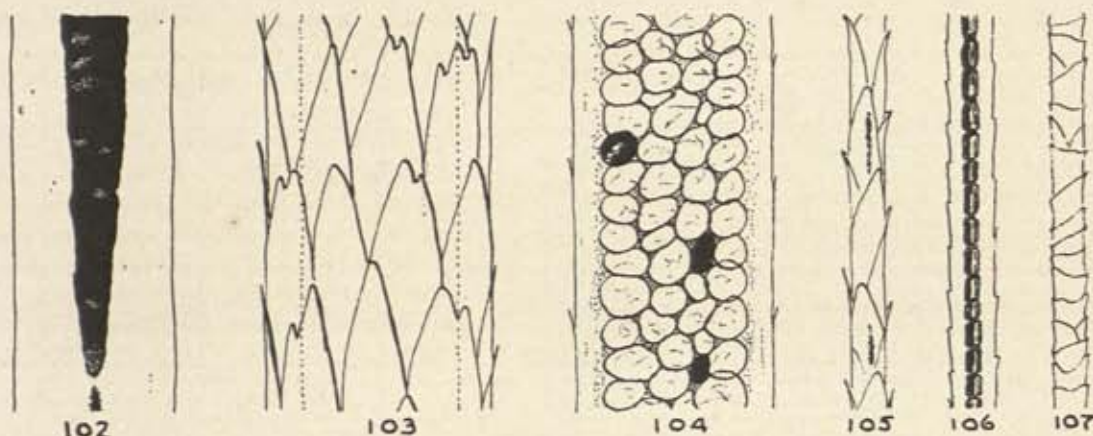
FIGS. 102 TO 107. *Urocyon cinereoargenteus scotti* (Mearns) ERW 2918.

FIG. 102..... protective... base..... 104 μ
 FIG. 103 detail of scales... protective... mid..... 144 μ
 FIG. 104..... protective... mid..... 128 μ

FIG. 105..... fur..... base..... 32 μ
 FIG. 106..... fur..... mid..... 28 μ
 FIG. 107..... fur..... distal..... 20 μ

scales in that genus. From *Canis* the pigmentation of the fur hair in that genus and the generally coarser protective hair will serve. From *Alopex* in the summer pelage the generally light pigmentation in *Alopex* is practically diagnostic. From *Felis* the scales will point the way.

UROCYON

The Grey Foxes

PROTECTIVE HAIR

COLOR: usually grizzled black and white, dirty white on belly, occasionally reddish on flank or neck.

LENGTH: usually up to 7 or 8 cm, rarely to 10 cm.

DIAMETER: 140 μ –268 μ ; mean 189 μ .

SCALES: the cuticular scales are generally prominent through the shaft except for the very tip. They are strongly elongated and have smooth margins except for a notch at the apex. *Indices:* base 0.46 (152 μ), basal 0.39 (148 μ), mid-section 0.46 (144 μ), widest part 0.10 (228 μ).

CORTEX: faintly stained yellow; pigment granules dark brown; fusi not uncommon.

MEDULLA: *index:* 0.74 (0.63–0.80).

Form: continuous, rarely assuming the *Lynx*-like form as in *Vulpes*.

Pigment: present.

FUR HAIR

COLOR: colorless.

LENGTH: about 3 cm.

DIAMETER: 24 μ –40 μ ; mean 30 μ .

SCALES: easily seen, smooth margined. *Indices:* 1.4 (28 μ), 0.7 (36 μ).

CORTEX: free of stain and pigment.

MEDULLA: *index:* 0.53 (0.37–0.62).

Form: as in *Vulpes* q.v.

Pigment: absent.

IMPORTANT CHARACTERISTICS

From *Taxidea*, with which the hair might be confused in gross aspect, the scalation will serve to identify *Urocyon*. From the other *Canidae* the important characteristics are noted in the foregoing key. The peculiar medulla of *Lynx* will serve to separate that genus from *Urocyon*.

ALOPEX

The Arctic Fox

PROTECTIVE HAIR

COLOR: white, or dirty brown, rarely slate grey.

LENGTH: 7 to 8 cm.

DIAMETER: 56 μ –132 μ ; mean 85 μ .

SCALES: like *Vulpes* q.v. *Indices:* base 0.78 (52 μ), widest part 0.32 (88 μ).

CORTEX: faintly stained yellow; no pigment in white hairs. (I have not examined summer or slate-colored specimens.)

MEDULLA: *index:* 0.61 (0.33–0.76).

Form: continuous.

Pigment: large dark brown granules scattered between cells.

FUR HAIR

COLOR: white.

LENGTH: 2–3 cm.

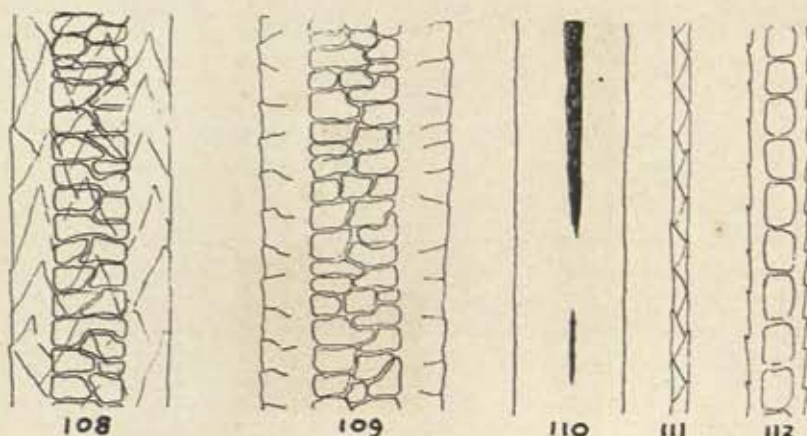
FIGS. 108 TO 112. *Alopex lagopus ungava* (Merriam) AMNH 19481.

FIG. 108.....	protective...basal.....	100 μ	FIG. 110.....	protective...distal.....	72 μ
FIG. 109.....	protective...mid.....	120 μ	FIG. 111.....	fur.....base.....	12 μ
FIG. 112.....	fur.....mid.....	32 μ			

DIAMETER: 20 μ –60 μ ; mean 30 μ .

SCALES: smooth margined. Indices: 1.6 (20 μ), 1.0 (36 μ).

CORTEX: free of pigment and stain.

MEDULLA: index: 0.57 (0.40–0.69).

Form: as in *Vulpes* q.v.

Pigment: absent.

IMPORTANT CHARACTERISTICS

The following will separate the hairs of *Alopex* from those of *Thalarctos*: the diameter of the protective hair of *Thalarctos* is much greater, while the proportionate diameter of the medulla is much less than in *Alopex*.

The following will separate the hairs of *Alopex* from *Lepus*: the medulla of *Lepus* is easily recognized by its "ear of corn" appearance and occupies over 80 per cent of the shaft.

CANIS

The Dogs, Coyotes and Wolves

PROTECTIVE HAIR

COLOR: variable, usually grizzled in wild species.

LENGTH: up to 7 cm.

DIAMETER: 156 μ –228 μ ; mean 191 μ .

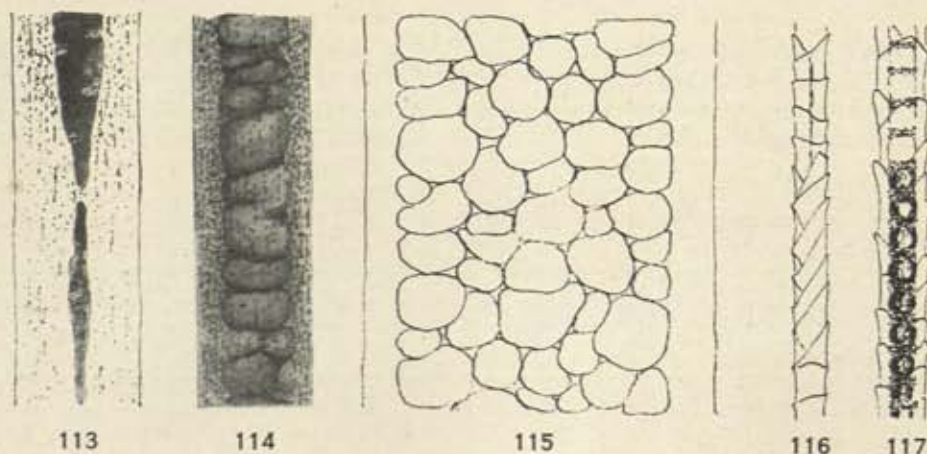
FIGS. 113 TO 117. *Canis nebrascensis nebrascensis* (Merriam) ERW 770.

FIG. 113.....	protective...base.....	80 μ	FIG. 116.....	fur.....base.....	20 μ
FIG. 114.....	protective...basal.....	76 μ	FIG. 117.....	fur.....mid.....	32 μ
FIG. 115 all pigment omitted.....	protective...mid.....	228 μ			

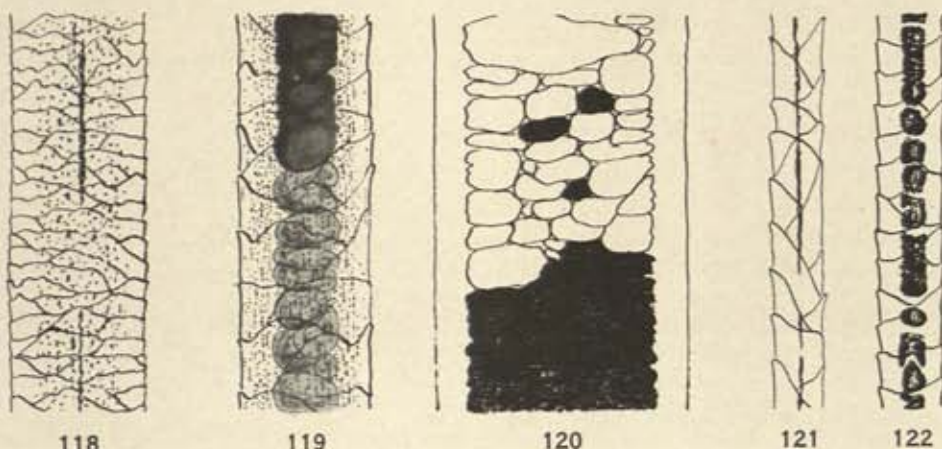
FIGS. 118 TO 122. *Felis oregonensis hippolestes* (Merriam) CMNH 2776.

FIG. 118.....	protective.....base.....	84 μ	FIG. 120.....	protective.....mid.....	164 μ
FIG. 119.....	protective.....basal.....	84 μ	FIG. 121.....	fur.....basal.....	32 μ
FIG. 122.....	fur.....		FIG. 122.....	mid.....	40 μ

SCALES: like *Vulpes* q.v. *Indices*: basal 0.21 (160 μ), mid-section 0.10 (180 μ).

CORTEX: stained dirty yellow to reddish brown; pigment granules dark brown in dark parts of shaft.

MEDULLA: *index*: 0.69 (0.55–0.88).

Form: continuous, tapers sharply at base.

Pigment: present.

FUR HAIR

COLOR: colorless to dingy brown.

LENGTH: about 4 cm, wavy.

DIAMETER: 28 μ –100 μ ; mean 55 μ .

SCALES: easily seen. *Indices*: 1.25 (36 μ) to 0.15 (96 μ).

CORTEX: free of pigment, sometimes stained.

MEDULLA: *index*: 0.48 (0.28–0.65).

Form: as in *Vulpes* q.v.

Pigment: intercellular clusters of dark brown granules.

IMPORTANT CHARACTERISTICS

There are no clear-cut characteristics that will infallibly separate the hair of *Canis* from that of the rest of *Canidae*. However the combination of characters given above seems to be reliable.

FELIDAE

FELIS

The Large Cats

PROTECTIVE HAIR

COLOR: tawny; darker hairs occur on some southern species.

LENGTH: about 6 cm.

DIAMETER: 132 μ –208 μ ; mean 167 μ .

SCALES: flattened, crenate. *Indices*: base 0.14 (84 μ), basal 0.42 (84 μ), widest part 0.07 (172 μ).

CORTEX: stained light yellow, filled with translucent granules of orange-brown pigment.

MEDULLA: *index*: 0.62 (0.47–0.70).

Form: continuous.

Pigment: absent.

FUR HAIR

COLOR: pale buff.

LENGTH: 3 cm.

DIAMETER: 28 μ –112 μ ; mean 58 μ .

SCALES: smooth margined, slightly elongate in basal portion. *Indices*: basal 1.3 (32 μ), mid-section 0.28 (48 μ).

CORTEX: as in protective hair.

MEDULLA: *index*: 0.42 (0.25–0.47).

Form: continuous column of cylindrical plinths, often fragmentary toward tip.

Pigment: present.

IMPORTANT CHARACTERISTICS

The orange-brown pigment granules and the dimension of the hair will usually be found satisfactory for identifying the hair of this genus within our range.

LYNX

Bob-cats

PROTECTIVE HAIR

COLOR: generally grizzled grey, brown and black.

LENGTH: 5 cm.

DIAMETER: 88μ – 184μ ; mean 152μ .

SCALES: slightly flattened with a wavy margin.

Indices: basal 0.14 (88μ), widest portion 0.04 (176μ).

CORTEX: stained yellowish, well supplied with dark brown granules.

MEDULLA: *index*: 0.75 (0.67–0.83).

Form: continuous, composed of very large globose cells that occupy the full diameter of the medulla between which are packed thin wafers of material that may be collapsed cells.

Pigment: very fine granules present.

FUR HAIR

COLOR: greyish or light buff.

LENGTH: 4 cm.

DIAMETER: 16μ – 40μ ; mean 27μ .

SCALES: prominent, smooth margined, elongate, especially toward the base. *Indices*: 1.05 (20μ), 0.67 (24μ).

CORTEX: free of stain, rarely with a few pigment granules.

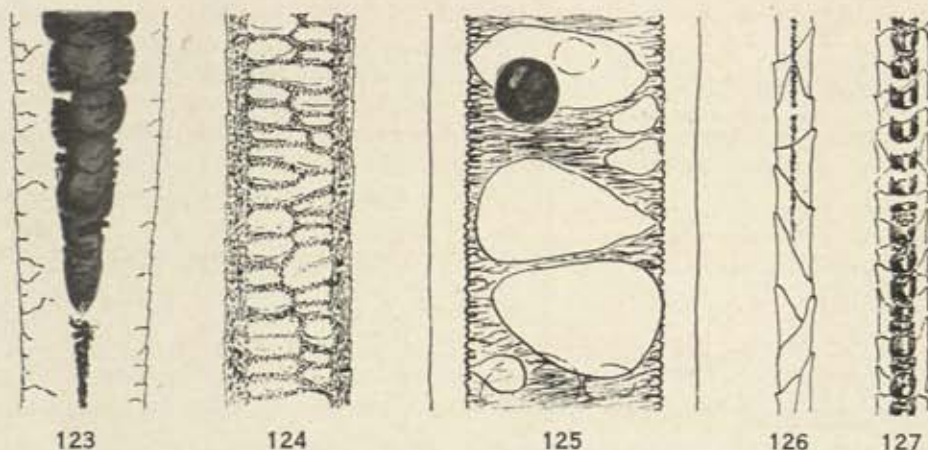
MEDULLA: *index*: 0.55 (0.37–0.70).

Form: same as *Felis* q.v.

Pigment: intercellular clusters of dark brown granules.

IMPORTANT CHARACTERISTICS

The peculiar structure of the medulla coupled with the diameter of the shaft is diagnostic for the protective hairs of *Lynx*.



FIGS. 123 TO 127. *Lynx baileyi* (Merriam) ERW 751.

FIG. 123	protective...base	76 μ –100 μ	FIG. 125	protective...mid	172 μ
FIG. 124	protective...basal	80 μ	FIG. 126	fur...base	20 μ
FIG. 127	fur...mid	32 μ			

THE EFFECT OF EARLY AND LATE BRAIN INJURY UPON TEST SCORES, AND THE NATURE OF NORMAL ADULT INTELLIGENCE

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ABSTRACT

This paper presents an hypothesis concerning the nature of normal adult intelligence. The hypothesis is based in part on the recognized clinical fact that brain injury affects test scores unequally, and in part on the apparent fact that this is less true of injury in early infancy: early injury, that is, may have a less selective and more generalized effect than late injury. The purpose of this review of the effect of brain injury on test scores is first to establish that there is such a difference in the effects of early and late brain injury, and secondly to show that the difference has meaning for the theory of intellectual development. It is proposed therefore (1) to examine the evidence concerning the effect upon test scores of late injury, without aphasia, and (2) with aphasia; (3) to compare these effects with that of birth injury, as far as they are comparable; and (4) to present an hypothesis of the development and retention of intelligence.

The hypothesis had its origin in the apparently isolated clinical problem of trying to account for certain high test scores made by patients with large cerebral destructions, but it has been found also to account for certain features of normal intelligence, and particularly for some of the characteristics of senescence.

THE EFFECT OF LATE INJURY OUTSIDE THE SPEECH AREAS

SINCE the characteristics of aphasia are so unlike those of non-aphasic deterioration, the test scores made by aphasic patients will be considered in a separate section. For the effect of brain injury without aphasia, there are several sources of information. One is the fairly large number of cases of brain operation in which the Stanford-Binet has been used, sometimes both before and after operation. Although there are serious drawbacks to its use for the purpose, the high validity of much of its content with normal subjects gives a special interest to the scores of brain-operated patients.

¹ Acknowledgments are due to Drs. Wilder Penfield, W. V. Cone and Arthur Elvidge for assistance and advice in the study of cases at the Montreal Neurological Institute; to Dr. Heinz Werner for further case material from the Wayne County Training School; and to Dr. Edgar A. Doll, Prof. K. S. Lashley and Prof. G. Humphrey for assistance and criticism in the preparation of this paper.

STANFORD-BINET SCORES IN CASES OF BRAIN OPERATION

I have been able to find reports of Stanford-Binet *IQ*'s after adult brain operation in 15 cases reported by the following authors: Ackerly (1935; the statement that the patient's score was "as good as the average" is taken to mean an *IQ* of 100); Brickner (1936); German and Fox (1934); Halstead (1940); Nichols and Hunt (1940); Lidz (1939); Penfield and Evans (1935); and Rowe (1937). This excludes non-surgical cases and children. The mean *IQ* for this group of 15 patients is 108, with scores ranging from 82 to 139 (not much weight can be given to the exact figures since in some cases the old Stanford-Binet was used, in others the new). In addition, I have records² of 23 patients examined at the Montreal Neurological Institute with the new Stanford-Binet; the average here is 107, with scores ranging from 54 to 152. For the total group of 38 cases the mean score is 108. Since the true norm for adults is probably below 100, there is evidently some selection operating to give us an above-average group—how much above average, in original level, there is no way to tell.

Again, five of the writers cited above give pre- and post-operative scores. In none was there post-operative loss. For 14 cases from the Montreal Neurological Institute with pre- and post-operative examination there was a mean loss of 1.3 points in *IQ* following operation. For the total group of 19 cases the mean drop in *IQ* is 1 point, the individual results ranging from a loss of 14 points to a gain of 11 points. Of the 19 cases, 7 show a loss, 6 a gain, and 6 no change following operation. Is this apparent lack of effect due to the compensating removal of dysfunction, with the effect of surgical destruction balanced by recovery from the pre-operative disturbance? To some extent, presumably; but in the cases from the Montreal Neurological Institute the pre-operative status was good (in each case the operation was

² Some of these cases have been reported elsewhere (Hebb, 1939, 1939a, 1941; Hebb and Penfield, 1940).

for the purpose of removing scar tissue), and the case reports of other writers suggest the same thing. The data do not give an exact knowledge of the effect of cerebral destruction, *per se*, but they do suggest strongly that destruction outside the speech areas has no great effect on Binet score. We shall see later that this is not confined to cases of smaller excision.

ANALYSES BY WEISENBURG AND MCBRIDE AND BY RYLANDER

Actually, the Binet-type test measures a number of abilities, and two important studies show the necessity of considering these abilities separately. Weisenburg and McBride (1935), in a study incidental to their larger work on aphasia, and Rylander (1939) have made extensive analyses of test abilities following cerebral injury.

In both studies the anatomical data leave something to be desired for the purpose of relating the defects to the type and extent of destruction. Weisenburg and McBride's group apparently consisted mostly of cases of diffuse pathological destruction due to vascular change and 19 of their 22 subjects were hemiplegic. Rylander's were all cases of operative lesion, but his case reports show definitely that a number of the patients examined had more or less extensive areas of pathological destruction in addition to the surgical removal: the 32 cases included cases of incomplete tumor removal, cases of infiltrating tumor (which usually recur and which are especially effective in causing mental changes), and one case in which the anterior cerebral artery was believed to have been shut off at operation. Weisenburg and McBride's work, therefore, is primarily a study of the effect of diffuse pathological destruction, the extent of which is not known; Rylander's a study of the effect of frontal pole removal together with an unknown amount of pathological destruction.

The importance of these studies is partly due to their use of good normal control groups, as well as to the fact that their analysis of the mental change is based on the independent measurement of a number of abilities. Rylander apparently succeeded in matching his clinical group very closely for age, occupation, and education. Weisenburg and McBride were able to match their right-hemisphere, non-aphasic group for age only; this makes for difficulty in fixing the amount of absolute loss, but not in fixing the loss in one ability relative to another.

The first question to be asked concerns the effect of cerebral injury on vocabulary score, which ap-

pears to stand in a special category in relation to mental deterioration. It seems unaffected in schizophrenia; at any rate, it is likely to be the highest score relative to normal levels (Babcock, 1930). In the gradual loss of test ability with age, it again remains the highest, or one of the highest, abilities (Jones and Conrad, 1932; Weisenburg, Roe and McBride, 1936; Wechsler, 1939), and Shakow and Goldman (1938) have shown that this is probably a retention of original adolescent level up until the sixties. Vocabulary is commonly found to be the highest score on the Stanford-Binet in adults who give evidence of mental loss following gross brain injury.

Direct evidence on the effect of frontal lobe injury on vocabulary is given by Rylander, who found no significant difference in the scores of normal and frontal lobe groups. The evidence of Weisenburg and McBride is in agreement; apart from tests of academic achievement, oral vocabulary score is the highest in the averages of their right-hemisphere group and about on a level with occupational and educational indices. Rylander's data actually make a slight loss probable, and Shakow and Goldman show that there is loss with advanced age over sixty. Vocabulary therefore is retained nearly at a normal level in deterioration, but is not completely unaffected.

When it is asked what tests, on the contrary, show the greatest effect with cerebral injury, it is harder to give an answer. Rylander unfortunately used no speeded non-verbal test which, from the indications of senescence and of schizophrenic deterioration, should show the greatest effect. Weisenburg and McBride did not have speeded non-verbal tests sufficiently sensitive for their normal group, but did find that right-hemisphere lesions depressed performance in those that were used. There seems to be no simple classification of kind of test score most affected in these studies. Rylander, for example, finding no effect on oral vocabulary, found also a loss of ability to give differences between abstract words. On the surface, at least, these results are hard to reconcile. Weisenburg and McBride, again, found the greatest effect shown by a purely verbal, unspeeded task, the Kelley-Trabue Language Completion; the next greatest in an unspeeded non-verbal task, the Porteus Maze. It seems likely that individual differences (of original test-score pattern) confuse the results. It is also likely that the locus or type of lesion may be important. One ability may be affected more by temporal-lobe than by frontal-

lobe lesions; another more by epileptoid dysfunction than by simple loss of tissue. Weisenburg and McBride's group was anatomically dissimilar to Rylander's, and neither was anatomically homogeneous. It is probably too much to expect, from what is known at present, that the picture of deterioration in anatomically different cases will be very similar. It is only surprising that we can name one ability—vocabulary—that consistently remains near its original level in deterioration. No similar generalization seems possible concerning the abilities or kind of ability affected most.

INDIVIDUAL CASES OF LARGE LESION OR MARKED DETERIORATION

The evidence discussed so far has been from cases of diffuse pathological destruction or relatively small surgical removals, and cases in which deterioration is not outstanding but evaluated by taking averages for large groups. Another approach to the question of the effect of brain damage is found in cases of unusually large surgical destruction or cases in which there has been marked deterioration.

The outstanding case is that of Rowe (1937). Dr. Rowe, in a personal communication, has furnished further details of the Stanford-Binet examination of his patient after removal of the entire right hemisphere above the basal ganglia. These details are very valuable. Dandy (1928), Gardner (1933) and O'Brien (1936) have reported cases which are similar surgically, but without psychometric examination. In such cases the bare statement that the patient showed "no obvious mental defect" must be particularly unconvincing to a psychologist, and a common-sense appraisal of intellectual ability may be especially fallible after brain injury (Hebb, 1939). Yet for certain aspects of intelligence it is impressive to find independent observers reporting that there was little or no mental change after operation. The repeated statements of relatives or acquaintances that they found no defects cannot be wholly dismissed: they indicate that some of the components of adult intellectual ability are at most slightly affected. The psychometric data given by Rowe support this strongly. His patient had unfortunately become sensitive about her intellectual powers (after loss of half the cerebral cortex!) and was also found to tire very easily; the examination was not completed, but the results, while they do not make it possible to calculate an *IQ*, are of great significance.

The examination (with the old Stanford-Binet) was begun with Year XVI, test 3, "Differences between abstract words". The test was solved "very readily", and the examiner shifted to Year XVIII. A score of 46 with one vocabulary list was made. "She was able to repeat one out of the series of eight digits forward, and one of the seven reversed. Her summaries for both of the (memory) passages in test 4 were judged satisfactory. Her solution of test 6 was correct in (b)."

This was the third time the test had been given the patient (others before the complete hemidecortication), but more than a year had elapsed since the second examination, and it seems impossible to explain such a performance by practice effect, in the presence of any serious, generalized intellectual loss. The repetition of digits, forward and backward, should alone be enough to show that for some things the patient's abilities were above the average for the general population. It is clear, of course, that these data do not mean that other abilities were unaffected. We have already seen that the retention of one ability does not mean that others are also equally retained, and the psychometrist's report, that the patient "fatigued fairly rapidly, both physically and mentally" is positive evidence that in certain other tests the patient would have made lower scores. The significant fact here is the objective evidence supporting the clinical opinion that the patient's abilities were in some respects well retained; and the fact that even if other test abilities were impaired the patient still had average or above-average ability in the kind of task which is the core of the Binet test. Such things as comprehension of words, differentiation of abstract terms, memory for complex verbal material and solution of reasoning problems, are the kind of task which is most successful in differentiating various levels of intellectual development in normal subjects.

In Rowe's case the cerebral destruction was, of course, unilateral. In the following case from the service of Dr. W. V. Cone of the Montreal Neurological Institute, the destruction was not as large nor as well defined, but was on the other hand bilateral; and an extended examination was carried out although visual defects prevented the use of some test material.

Case 1.—H. D.; 15 yrs. 11 mos.; male, right-handed. The patient had a history of drainage of brain abscess in the right temporal region, with transient hemi-paresis, followed by epileptic attacks and gradually impaired vision. Two more abscesses were reported to have been drained, "a

pint of pus" from one of them, followed again by left hemi-paresis and complete blindness. The parents reported that he had become "slightly dull" mentally at this time.

On admission in April, 1939, an encephalogram showed a "huge right-sided expanding intracranial lesion" in the right temporoparietal region. Drainage of multiple abscesses, before and behind the foot of the central fissure, was done by Dr. Cone two days later, followed by treatment with sulfapyridine. In the following four months there was a gradual increase of voluntary movement of left arm and leg, and some recovery of vision. Three months after operation, 1 month before examination, there was a grand mal attack.



FIG. 1.

A post-operative encephalogram (Figs. 1 and 2) showed him at this time to have a very large defect of the right hemisphere, and a smaller defect of the left. The ventricle was in communication with the subdural space in the right hemisphere in its dorso-parietal aspect. Dr. Arthur Childe, radiologist, and Dr. Cone agreed on stereoscopic study of the X-ray plates that the destruction on the right side was certainly 40 per cent, possibly 50 per cent of the total mass of the right hemisphere, and that the destruction of the left (by pressure only) was at least 20 per cent of the left hemisphere. This would mean a diffuse destruction of 30 to 35 per

cent of the mass of the cerebrum—20 to 25 per cent on the right, 10 per cent on the left side. Since the estimation of quantity was difficult, it may be said that the destruction was not less than 20 per cent, and probably more than 25 per cent of the mass of the cerebrum, with an upper limit of probably 35 per cent, possibly as high as 40 per cent.

The patient's psychological status appeared to be exceptionally good. The one defect, by informal observation, was his inactivity, and apparent willingness to do nothing for rather long periods. But in conversation he seemed normally alert and responsive, and quite co-operative. His memory was good; he knew the names of nurses who spoke to him, and after being told the examiner's name once remembered it readily the next day. He knew the date, the name of the hospital and the city he was in; the name of the present king of England, George VI, of the preceding king (Edward VIII) and the approximate date of George V's death. He answered questions about approximate distances of his home from other cities correctly and readily.

Psychometric examination was limited by his almost complete visual defect. The Stanford-Binet, form L, was given, omitting tests involving vision. The vocabulary score was 21, at the Average Adult level, and he succeeded with two tasks at a higher level, the repetition of 8 digits forward (SA II) and 6 digits backward (SA I). At the Average Adult level, in addition to the vocabulary success, he succeeded with differences between abstract words and repetition of sentences. At Year XIV, he failed the Orientation test, but succeeded with Ingenuity and Abstract Words. At Year XIII he succeeded with the two non-visual tasks, Problems of Fact and Memory for Words; at XII, failed one of 4 non-visual tasks, the Verbal Absurdities; at XI, succeeded with all non-visual tasks; at X, failed one, Finding Reasons; and at IX, succeeded with the four non-visual tasks.

From the Weisenburg and McBride battery, he was given the Oral Analogies test, making a score of 9; and Oral Opposites, with a score of 14, time score 120 seconds. These three scores fall near the lower limits of Weisenburg and McBride's normal range; the repetition of digits, forward and backward, and probably vocabulary and difference between abstract words, are above average by the same norms.



FIG. 2.

One speeded test, the "Tactile Formboard" (experimental, test-retest reliability of 0.70 only), independent of vision and standardized for the use of one hand, was given. Here again his score was at the lower quartile of a normal group.

There are some grounds for making an estimate of the original level of ability in this patient. There is first the vocabulary score, and the fact that answers in this test were given promptly and without evidence of difficulty of expression with words which the patient understood. There was no "scatter" (if the term may be used here) in the test: there was success with the first 17 words, with a prompt, but wrong, definition of the eighteenth ("Priceless: not worth anything"), and success with the nineteenth, "Disproportionate"; no. 20, the patient said he didn't know; no. 21, "shrewd", was defined wrongly; "tolerate", no. 22, could not be defined; no. 23, "stave", was correctly defined as part of a barrel; no. 24, "lotus" was first unrecognized, then the patient said it might be a flower; no. 25, "bewail", was defined correctly; and no further successes were obtained. The pattern of success and failure seemed to be that of a normal individual. The performance of

a patient was not to be distinguished qualitatively from that of a normal subject of the same level. He was alert and responsive throughout. These considerations make it probable that the score of 21 on the new Stanford-Binet vocabulary list is fairly representative of the original level of the patient. It corresponds to an *IQ* slightly above 100. The school record, as given by the patient's mother, also corresponds. He passed into grade VII at the age of 14, having failed once in grade VI. He "hated school", but seems to have done reasonably well there—with an average record for the son of not very intellectually-inclined parents, in a small country town.

It appears then that in repetition of digits, forward and backward, in memory for sentences, differences between abstract words and "Ingenuity" the patient also retained something close to the original level of ability after diffuse loss of 20-40 per cent of the mass of the cerebrum. The value of the case is to be found in its combination of a really extensive lesion, involving the left as well as the right hemisphere, with an unusually good retention of subjective clarity, responsiveness, memory and apparent coherence of thought processes,

as far as these were evident in his conversation. In the examiner's judgment, these aspects of intelligence were unaffected, and there is support for this opinion in the Stanford-Binet record.

The cases just discussed had their special interest because of the retention of certain attributes of intelligence—responsiveness, powers of directed effort, comprehension of verbal material and memory—in spite of exceptionally large cerebral lesions. Occasionally the retention of these abilities is of special interest not because of the size of the patient's injury, but because the injury has induced a sharp loss in other abilities. When the psychologist has an opportunity to examine such a patient, he knows at least that he is dealing with a brain injury which is capable of seriously affecting "intelligence". In such circumstances, manifestations of superior ability, even in a single case, are significant. The following case is that of a patient operated on by Dr. Arthur Elvidge at the Montreal Neurological Institute.

Case 2.—M. G.; female; 46 years of age; partial removal of bilateral oligodendroblastoma in the frontal region, with post-operative confusion, defects of immediate memory and euphoria. At operation Dr. Elvidge made a right frontal pole amputation, and estimated that about two thirds of the tissue of the frontal lobes was destroyed by the neoplasm and the surgical procedures. The neoplastic tissue could not be completely removed because of the patient's condition. Dr. Elvidge believed that the right, and possibly both anterior cerebral arteries were clipped at operation.

Following operation, with deep X-ray therapy, there was marked improvement in the patient's condition. There were no sedatives given during the period of psychological examination, (third and fourth weeks after operation) but the X-ray therapy and the frequently high intra-cranial pressure undoubtedly contributed to the post-operative confusion. The patient was "cheerful to excess", alert and co-operative until the time of discharge to another hospital, four weeks after operation. There were also signs of facetiousness, but this and the slight euphoria had decreased somewhat by the fourth week. About two years after operation it was reported that the patient was much better and doing her housework, but no details were obtained.

The only formal psychological test used was the Stanford-Binet, form L, omitting tests involving vision, because of the patient's low acuity (6/30). The vocabulary score was 26, at the Superior Adult II level—the only success at this level. At

Superior Adult I, the patient added success with Sentence Building; at Average Adult, Memory for Sentences; at Year XIV, Ingenuity, Orientation and Abstract Words II. Below this level all non-visual tests were plus. So far this is the record of an intelligent person. But other aspects of intelligence were sharply affected: more so when the intracranial pressure was high, but still affected when it was not. Lying near large windows which lighted the ward during the day, the patient could not say whether it was day or night. She was usually unable to say whether it was winter or summer, what part of the day it was, or whether she had had her lunch, although the tray might have been taken away only a few minutes before. These are the phenomena of "loss of immediate memory", but there is something more than memory involved here. The patient's vision was adequate to a description of the details of the Stanford-Binet picture absurdities, but until she was asked to describe them she did not detect the absurdity; then only in some of the simpler pictures. Her vision was certainly enough to let her see whether the window was the source of light or not, but did not tell her whether the time was day or night.

On the other hand, the patient had an excellent immediate memory for some things. The name and the distinctive step of the examiner was remembered, and the names of several of the house staff. She was oriented as to place most of the time—the Neurological Institute was the "Neuro-something Institute", although at other times she thought she was in a small hospital near her home.

In such a case the mental defect is restricted. Unfortunately, the patient was discharged to another hospital before other tests were used, and with these a somewhat wider zone of defect might have been shown. In any case, it would be hard to draw a line of demarcation about the region of intellectual loss. The facile explanation by loss of immediate memory is not satisfactory. On the one hand, immediate memory for some things was good; on the other, something more than memory was involved. No normal individual in a room lighted by a large window would have trouble knowing that it was day and not night. As in other cases in which at first glance there appears to be a simple loss of one function with retention of others, closer examination shows that this is not so. We have not yet found the conceptual categories for the description of behavior, which will allow us to say that this ability is affected alone, or that one ability is gone completely while others are

retained. The tests available for the analysis of mental ability are impure and the relation of test abilities to the brain probably not such that injury can eliminate one without affecting others. The phenomena of the case just reported are not unusual; what is less common is the extent of the contrast between the subject's mental activity, alertness and retention of certain test abilities, on the one hand, and her serious intellectual disability in another field.

SUMMARY OF TEST DATA IN NON-APHASIC CASES OF DETERIORATION

The evidence from the larger groups of cases, and from the individual cases cited here, agrees on one point. Ability to do certain tasks which form an important part of Binet-type tests may not be greatly affected even by large injuries to the mature brain: these tasks include word definition, comprehension of and memory for complex verbal material, and the solution of unspeeded verbal problems which are hard to classify apart from the fact that they appear to be of a familiar kind, dealing with matters of general significance (though even this may not be true in all instances). The evidence shows also that there is likely to be deterioration in other abilities, although the extent and kind of loss in any individual case is unpredictable. The particular tests which have been found to show the effect of late brain injury, in the various cases cited, include: maze tracing, sentence completion, differentiation of abstract words, giving of opposites, analogies, speeded block-manipulation tasks, and picture absurdities.

Vocabulary is most noteworthy as an ability which is at most slightly affected; in all probability there are other things which are as well retained, but which are not measured directly by existing tests. This is suggested by the repeated and emphatic clinical statement that "intelligence" has been unaffected by surgical removal of cerebral tissue. The statement cannot be taken at face value, but it is presumptive evidence that important components of normal adult ability are well retained.

THE SPECIAL CASE OF APHASIA

This paper is not concerned with the question whether aphasia involves a loss of "intelligence" or not. The question is still the subject of controversy, partly because the various writers obviously have different ideas as to what intelligence

is. Head's conception, that aphasia involves defects of symbolic formulation and expression, seems generally accepted: on the face of it, this is an intellectual defect, and has been so interpreted by some writers. But others, who have been able to show that the aphasic may be very competent in some matters involving intelligence, argue that only a special power and not intelligence is lost. The argument makes intelligence a unitary thing, which is retained or impaired as a whole. In normal individuals, this may be an acceptable point of view; for clinical subjects it is untenable. The evidence already reviewed shows that it is possible after brain injury to have sharp loss of one ability side by side with a high level in others. This paper therefore is concerned with the nature of the actual test scores made in aphasia, not with the meaning of possible defects, or with the question of how "intelligence" is to be defined.

In one point, however, it will be desirable not to take test scores at their face value. Kennedy and Wolf (1936) have pointed out that many of the so-called non-verbal tests used in the study of aphasia are not, in fact, non-verbal, but involve understanding the language of the instructions. The task is non-verbal, but the method of directing the subject is not. If he only partly understands the directions or is slow in understanding them, he may be seriously handicapped.

To minimize this difficulty of method, tests are desirable in which there is (1) a practice period in which the examiner can make sure that the subject knows what to do, and has adjusted himself to the task; (2) a graduated series of tasks of the same kind as those of the practice series, in which no new directions are given, and in which success with the first, easy items would show that the practice period had achieved its purpose. It would also be desirable to have (3) some tests in which speed is unimportant, as a further guarantee that low scores are not due merely to a slow adjustment by the subject.

The chief source of psychometric data on aphasia is the study of Weisenburg and McBride (1935). This study was handicapped by a lack of suitable non-verbal tests, and therefore the results are open to the criticism of Kennedy and Wolf. Nonetheless Weisenburg and McBride make it improbable that the low non-verbal test scores of aphasic patients are due only to failure to understand directions. Some of their tests partly meet the requirements I have suggested above: the Seguin Form Board, in which the subject has three trials, his score being the time for the most rapid

solution only; the Knox Cube test, and the Porteus Maze, both unspeeded and graduated from easy to hard, but without practice periods. If errors in these two latter tests were made only with the later and more difficult items, success with the easier ones would show that failure was not due to mis-understanding the directions. Unfortunately Weisenburg and McBride do not touch on this point and do not give averages and distributions of scores in individual tests such as those mentioned, or in the Goodenough "Drawing a Man" test.

Some slight further evidence was obtained at the Montreal Neurological Institute, in the course of a preliminary study of the usefulness of an experimental test battery. The data were obtained from 6 cases only, and complete psychometric examination was not done.

Five were cases of "predominantly expressive" aphasia; one a case of amnesic aphasia. Three, including the case of amnesic aphasia, were cases of temporary speech disturbance, lasting from 2 to 10 months, following brain surgery in or near the speech areas; in each of the three, tests made when the aphasia was severe were repeated when it had almost disappeared. Some of the tests were in rough preliminary form, but cast light on the abilities of aphasic patients relative to a rather good normal control group of public ward patients.

Results.—(1) The Knox Cube test first, showed apparently no effect of the brain injury—a rather surprising result, since in this test verbalization appears to contribute to the success of normal individuals. The reliability of the test, however, is probably not high. (2) In a modification of the Picture Absurdity test of the Revised Beta Examination (Kellogg and Morton, 1934), using large, clearly drawn pictures, without time limit and with two practice items, all subjects were below the normal lower quartile. For two of the subjects the practice items may not have been effective, but the other four definitely understood what they were to do. (3) The Kohs Block test was given to four patients only. One of these, the case of amnesic aphasia, made a score of 127—above the upper quartile of the normal group; in the other three cases, with severe motor aphasia, very low scores were made, although in two there were definite indications that the task was understood. (4) Finally, in a block-manipulation test (as yet unpublished), with preliminary practice period, graduated series of tasks, and time limit rather than time score, there was definite evidence

of loss of ability with aphasia and a rise of ability when the aphasia had almost disappeared. The evidence indicated, however, that the loss was not very great, and the amnesic aphasic with a high score on the Kohs Block test made a high score here.

In summary, this group of 6 patients showed loss of ability in non-verbal tasks, which did not seem due to failure to grasp the instructions. In one non-verbal task, the Knox Cube, there was no evidence of loss (possibly due to low test reliability); in one, Picture Absurdities, loss seemed general, although it is possible that some subjects may have retained their normal level, if this was originally low; in two block-manipulation tests, some subjects showed much greater defects than others, one subject made high scores, and the amount of loss seemed to be not as great as with the Picture Absurdity test, but greater than with the Knox Cube.

These results are in one way the counterpart of those observed in cases of non-aphasic deterioration. There is a close similarity in the tendency toward a selective effect of brain damage. In one case verbal indices are chiefly affected, in the other non-verbal, but in both the psychograph is marked by an essential disparity of scores *that goes, in extreme cases, well beyond the normal range*. The similarity ends here. In non-aphasic deterioration it appears that some abilities are always retained near their normal level; in aphasic deterioration, although a few patients retain some other abilities at a high level, it seems probable that in a majority of cases there are no test abilities without definite deterioration. Kennedy and Wolf (1937) argue that this is because aphasia is apt to be complicated by an added intellectual deterioration not characteristic of aphasia itself, due to the occurrence of lesions outside the speech area as well as inside it. This may be so, and it is quite possible that in those patients whose test scores are all extremely low (a common situation with severe motor defects) we are dealing with *both* aphasic and non-aphasic defects simultaneously. Whatever the explanation, the facts seem to be (a) that in aphasia there is frequently a wide disparity of abilities, but also (b) that in most cases both verbal and non-verbal indices show evidence of loss.

In any case of adult deterioration, the disparity of abilities may be extreme. In aphasia, above average abilities may be found together with abilities below the normal adult range; in Case 2,

without aphasia, the same thing was observed, and the changes described by Goldstein (1936) suggest that the use of standard tests in his case would have shown a similar situation. This disparity of abilities in adult cases is to be contrasted with what is to be found in cases of birth injury.

TEST SCORES AFTER INJURY TO THE INFANT BRAIN

The discussion here is confined to cases of "birth injury" in which test-score levels are not primarily determined by sensory or motor defects. The patient with hemiparesis cannot carry out certain tasks properly because of his motor defect; his test score is not then representative of an intellectual level. As far as can be determined, the scores to be discussed were not directly affected by such handicaps.

This makes for a selected sample. Athetosis or hemiparesis is detectable, but a case of cortical destruction without gross symptoms may pass for normal. The known birth-injury population therefore may deviate systematically from the total birth-injury population, so that one cannot compare the average test score of the birth-injured with the average score in cases of adult injury. The unknown degree of selection in the clinical birth-injury population is the principal difficulty of this study, and I shall return to it again.

A less direct comparison may be made, however, through the pattern of test scores. We do not know that the birth-injury sample is representative; but we can ask whether the defects, *when they do occur*, are similar in cases of early and late injury. In adult injury there are two psychometric patterns: the non-aphasic syndrome, with vocabulary in particular high and other abilities low, and the aphasic syndrome, with non-verbal abilities markedly higher than verbal abilities. For all cases of adult deterioration there would be, therefore, a bi-modal distribution of vocabulary scores and of differences between verbal (Binet) and performance scores, one mode due to the inclusion of cases of aphasia, the other to cases of deterioration without aphasia. Are the defects due to early injury at all similar? The available data, in cases of birth injury, are for children or young adolescents, which is another difficulty in making a direct comparison; but it is possible to compare brain-injured children with normal children, and brain-injured adults with normal adults, to see if deviations from the normal in each case are of the same kind, and of the same extent.

By the kindness of Dr. Heinz Werner, I have obtained details of test data in a series of 32 cases of "exogenous" mental defect (Strauss, 1939; Werner and Strauss, 1939), from the Wayne County Training School. These are not even representative of the known birth-injury cases without gross motor handicap, since those with Binet *IQ*'s below 50 were excluded. As it happens, however, the selection here is on the safe side since it operates against the conclusions of this paper—namely, that certain test levels are lower with early than with late injury.

Werner's data include Stanford-Binet scores (in some of the cases the old, in some the new form was used); year level of vocabulary score; Stanford-Binet scatter; and Arthur Performance Test score. With these data I have included four comparable records from the Montreal Neurological Institute. Strauss has described the Wayne County Training School group as including only higher grade defectives, without gross motor handicap. The lack of motor disability makes an important difference between this group and that of Doll, Phelps and Melcher (1932), the object of whose study was of course different.

The chronological age range, in the combined groups, is from 10 to 19 years, and the range of Binet *IQ* from 43 to 99. Vocabulary scores are available for 32 of the 36 cases. Taking the maximal chronological age as 15, Table I gives

TABLE I

DISTRIBUTION OF VOCABULARY RETARDATION IN MONTHS, OBTAINED BY SUBTRACTING VOCABULARY AGE LEVEL FROM CHRONOLOGICAL AGE¹ IN 32 CASES OF BIRTH INJURY (DATA IN 28 CASES PROVIDED BY WERNER)

CA - VA ² (months)	No. of cases	CA - VA (months)	No. of cases
-12 to -1	1	60 to 71	9
0 to 11	1	72 to 83	3
12 to 23	1	84 to 95	5
24 to 35	1	96 to 107	1
36 to 47	4	106 to 119	3
48 to 59	3		

¹ Range of chronological age was actually 10 to 19, but 15 is taken as a maximum; vocabulary age ranged from less than 6 to 14.

² VA = vocabulary age.

the differences between chronological age and vocabulary age level. In one case only the vocabulary age is (6 months) higher than the chronological age; the median vocabulary retardation is between 5 and 6 years, the greatest 9 years.

This is evidence that vocabulary is generally depressed by birth injury. Vocabulary, also, does not tend, as it does with mature injury, to be one of the high Stanford-Binet subtest scores. Two of 30 cases have vocabulary at the highest year-level of successes; 10, on the contrary, have vocabulary scores at the basal age, and the rest are nearer the basal age than the highest year-level of successes. Scatter seems to be somewhat greater than with normal children, but with vocabulary scores tending to be low it is not like the scatter that may be found in adult cases.

TABLE II

DISTRIBUTION OF DIFFERENCES OF BINET AND PERFORMANCE IQ'S, OBTAINED BY SUBTRACTING PERFORMANCE IQ FROM BINET IQ, IN 32 CASES OF BIRTH INJURY (DATA PROVIDED BY WERNER): MINUS SIGNS INDICATE THAT THE PERFORMANCE IQ IS HIGHER ¹

Difference	No. of cases	Difference	No. of cases
24 to 20	1	- 1 to - 5	2
19 to 15	0	- 6 to -10	7
14 to 10	1	-11 to -15	9
9 to 5	3	-16 to -20	1
4 to 0	5	-21 to -25	3

¹ Range of Binet IQ's, from 50 to 99; of performance IQ's, 53 to 105.

Table II summarizes the differences between Binet and performance IQ's. These show, as others have observed, that the non-verbal IQ of the birth-injured tends to be higher than his verbal IQ. There is, however, no indication of a bi-modal distribution of differences. They range from plus 23 to minus 25; disregarding sign, from 0 to 25, with a median difference of 10 points in IQ. Arthur (1933, table XXV) gives median differences for normal children from 5.5 to 14.0; for children of the same range of IQ as those of the present group, a median difference of about 7.5. The median difference therefore is somewhat greater than normal, but the individual differences are within the normal range (see Arthur's table XXXIV, for example, for normal Italian and Jewish children, where the differences range from plus 23 to minus 36 for children whose Binet IQ's are below 100).

Obviously vocabulary is markedly depressed in these cases, and has not the relationship to other scores that is apt to be found in cases of adult deterioration. There is no evidence of a bi-modal vocabulary distribution, nor of a bi-modal distribution of the relationship between verbal and non-

verbal ability. The low level of vocabulary score means that the "non-aphasic syndrome" of the adult is not to be found here.

Nor does the adult aphasic syndrome appear. "Speech-area" injury in the infant may affect later symbolic formulation and expression: indeed, it is possible that the more extreme defects of imbecility or idiocy (not represented in the group analyzed) may be the result of injury to what, in the adult, is the speech area. But it is characteristic of aphasics to have some non-verbal abilities well within the normal range, with the verbal abilities outside the normal range: in a large proportion, with a marked discrepancy between verbal and non-verbal abilities. No writer has discussed, as far as I am aware, the occurrence of aphasia as the result of birth injury (as distinct from lesions occurring or progressing after speech has developed), but it appears that when verbal defects are as serious as those of aphasia the level of other abilities is not far removed. In short, the only children whose verbal capacities are as poor as in the ordinary case of aphasia would be imbeciles at least. Doll (1933) refers to the effect of birth injury upon speech, pointing out that speech defects may be accompanied by normal ability elsewhere, but he appears to mean a kind of defect which is not at all like the aphasic disturbance of symbolic function. Such defects are to be thought of as disturbances of speech production, not of the cortical processes underlying speech organization (just as there are adult speech disturbances which have no relation to aphasia).

It is well to make the point that the vocabulary ability of the birth-injured child is not depressed merely by a lack of opportunity or of normal experience. In three of the cases observed at the Montreal Neurological Institute information on this point was obtained.

The first (J. B.) was a young woman of 19 years of age, suffering from hydrocephalus which dated apparently from the age of 5 years. The patient made a score of 6 on the revised Stanford-Binet list (level of Year VI; *M.A.* 6-10; basal age VI, highest success at VIII). She attended school until the age of 13, and apparently lived a normal life at home until the time of entering hospital. The second (L. S.) was a girl aged 13 years, 1 month, with a history of birth injury and convulsions. She attended school, but did not learn to read or write; her mother, however, said that she helped with the housework at home. In

spite of this, she did not know what "eyelash" meant, nor "scorch"; "muzzle" she said was "muslin cloth". Vocabulary score 8 (Year VIII; *M.A.* 5-7; basal age IV-6, highest success at VIII). The third case (N. H.) is clearest of all; a girl aged 12 years, 2 months, with epilepsy following birth injury. The mother apparently devoted all her time to trying to teach the child and to train her as other children. She had been taught to sound simple words phonetically, and with a familiar book seemed to be able to read, although in fact she could only repeat the story by memory. She talked fluently, and no effort had been spared to bring her up normally. The vocabulary score was 7 (Year VII approximately; *M.A.* 6-8; basal age VI, highest score at VIII). If opportunity determined size of vocabulary, it would have led to a higher score in this case.

Finally, a case reported by Bradley (1937) will be cited. It has a special importance in that the birth-injured child had an identical twin (case of Jim and Burton). There was no sensory or motor handicap, and the two boys grew up together and enjoyed being mistaken for one another. At the age of 13-2, one twin had a Stanford-Binet *M.A.* of 13-1 (*I.Q.* 98), the other of 6-7 (*I.Q.* 51). Vocabulary scores, with one list, were 28 and 12 respectively. This is exceptionally direct evidence of the effect of an early cerebral injury, with both environment and original potentiality controlled.

VALIDITY OF THE COMPARISON BETWEEN EARLY AND LATE INJURY

The psychometric data from these cases of exogenous mental defect make it appear that vocabulary, and other abilities tested by the Stanford-Binet, are depressed by birth injury. There is very nearly conclusive evidence that vocabulary and some of these other verbal abilities are not seriously affected by injury occurring at maturity, except in the case of aphasia; and aphasia itself is characterized, in a fairly large number of cases, by the rather high level of some non-verbal abilities, which again does not appear true of mental deficiency. Unless there is what Kennedy and Wolf consider to be a combination of aphasic and non-aphasic deterioration, adult brain injury is likely to leave some abilities at a nearly normal level. How valid is this comparison of test scores in cases of early and late injury?

The low vocabulary scores after early brain injury have been shown not to be due to environmen-

tal deficiencies. Another possible explanation can also be ruled out; that the lesions of infancy may be more widespread or more diffuse, involving possibly more dysfunction of the partly destroyed tissue, and that they are more deteriorating for this reason. From the evidence of Rowe's case of hemidecortication, and that of Case 1, as well as from the data of Weisenburg and McBride from their non-aphasic control group (essentially a group of cases of diffuse injury), it seems that diffuse destruction to the adult brain, like the clean-cut surgical removal, leaves certain verbal abilities at most only slightly disturbed. It is important to note that this is true even when other abilities are seriously disturbed indeed, as in Case 2: here surely the lesion was capable of affecting intellect—without greatly affecting vocabulary and some kinds of problem-solving. So in aphasia; some abilities are depressed to a degree that, with infant injury, is only found in extreme cases of mental deficiency. The conclusion drawn from the comparison is not that intellect is less disturbed by adult injury, but only that some things are less disturbed and that the defects resulting from early and late injury are qualitatively different. It may be—in fact, it seems likely—that in other abilities the effect of early injury is less than that of late injury.³

The real difficulty in making this comparison is the possibility of an unsuspected degree of selection in the birth-injury population studied.

If the effect of early and late injury is the same, the only way of accounting for low vocabulary scores in the birth-injured is by supposing that the known population have speech-area damage. This might happen in either of two ways: either the early injury tends to be bilateral, or only children with speech area damage are sufficiently retarded to be detected as clinical cases (since we are dealing with cases in which there are no gross motor or sensory disabilities). Since it is known that there is more restitution of function with infant than with adult injury to the brain, verbal abilities would tend to be low, but not as low as in adult aphasia. Such possibilities cannot be entirely dismissed, for the exact determination of site and

³ It would be easy to over-simplify the distinction between cases of early and late injury. Werner's qualitative analysis of exogenous mental defect has shown the existence of a kind of dis-organization which is strikingly similar in some respects to what may be found with certain kinds of adult injury. The contrast drawn here is between patterns of test scores only.

extent of injury with early lesions is a very difficult business, as Doll (1933) has pointed out.

It seems most unlikely that every detected case of infant injury, without gross motor defect, involves speech area damage, although this must remain, at present, as a possibility. Animal studies have consistently indicated that early damage is less deteriorating than late damage (*e.g.* Lashley, 1933; 1938; Tsang, 1937; Beach, 1938), and there is no experimental support for an opposed conclusion based on clinical evidence. It may be pointed out, however, that indices of animal intelligence have never been comparable to those of the standard intelligence test, which is concerned mainly with complex abilities developed during the whole period of growth rather than with the rate of acquisition of a new skill at maturity. Finally, it should be repeated once more that the tentative conclusion drawn from these clinical comparisons is that only a few abilities (of the many rated by standardized tests) seem to be retained better after late than after early injury to the human brain.

THE DEVELOPMENT AND RETENTION OF INTELLIGENCE

The weight of evidence points to a more widespread and less selective effect of the large infant injury than of the large adult injury. Unless known cases of exogenous mental defect involve lesions in the speech areas (the possibility already discussed), to account for the uniformly low vocabulary and verbal test scores, it must be that *low verbal test scores are produced by early lesions outside the speech areas*. With vocabulary at least it appears that a cerebral lesion may be deleterious at infancy and not at maturity, for such lesions at maturity do not affect vocabulary to a detectable degree. If this is so, the development and the retention of an ability may depend on the brain in different ways. An intact cerebrum is necessary for the normal development of certain test abilities, but not for their retention at a nearly normal level. In other words, *more cerebral efficiency or more intellectual power is needed for intellectual development than for later functioning at the same level*.

Stating the problem in this way suggests a clue to a possible solution. The actual modifications of behavior which occur in intellectual development are mostly qualitative. Faced with a complex situation, the subject sees it in a new way and makes a new response—not more responses or harder responses. Now often in such modifications of behavior it is the first steps which demand

intellectual capacity. Learning to solve a problem demands more intellectual effort than solving more problems of the same kind; this is obvious with formal problems, but it may also be true of the perception of relationships: in the figures used by the Gestalt psychologists, in puzzle pictures of the kind made to amuse children, in Street's Gestalt Completion test, there is ample evidence that the original perception of a relationship may make more intellectual demand than the same perception later. It is not far-fetched to suppose that this is also true of the perception of relationships in everyday events which the growing child does not set out consciously to master, as he must an arithmetic problem or a puzzle picture, but which make up the "problems" of everyday life. The intelligent child solves these problems without thinking of them as such, but nevertheless at a faster rate than the less intelligent: intellectual capacity must be important in the development and it is plausible to suppose that here, as in more formal intellectual undertakings, the first achievement is what requires the greater amount of intellect. The development of social appreciation, common sense and verbal comprehension, therefore, may demand an intact brain, while their retention does not.

Intellectual development then would involve stable, qualitative changes of behavior and perception, dependent for their first appearance upon more elaborate intellectual processes than for their later functioning. Physiologically, this implies that stable changes of neural organization may occur as the result of activity in other parts of the nervous system. Normal development of verbal comprehension demands an intact or almost intact cerebrum, but its persistence at a high level is possible after the removal of the right half of the cerebral cortex. This is accounted for on the supposition that the actual basis of the adult verbal response is in the middle regions of the left hemisphere (in right-handed individuals, of course), but that the physiological organization of this part of the brain is partly determined by earlier activities in the rest of the brain. The qualitatively good response is a modification due to an earlier and more elaborate kind of cerebral activity.

All this, however, emphasizes only one of the factors entering into test performance—the one accounting for high scores following mature brain injury. But verbal test indices, like non-verbal, vary in their susceptibility to the effect of injury outside the speech areas and no test is wholly un-

affected. The stable qualitative changes of intellectual development are therefore not all that is rated by intelligence tests. To a varying degree, the tests must also measure something closer to the intellectual power that produced the qualitative changes in the first place.

An hypothesis can now be stated, to account for the high level of certain test scores following late brain injury, for the varying degree to which other test scores are affected, and for the differences of the effect of early and late injury:

In any test performance there are two factors involved, the relative importance of which varies with the test: one factor being present intellectual power, of the kind essential to normal intellectual development; the other being the lasting changes of perceptual organization and behavior induced by the first factor during the period of development. Roughly, the one concerns power of "reasoning", of synthesis and invention; the other skill (that is, a factor due to experience). The term "present intellectual power" is not altogether satisfactory; it is used in a special sense not equal to "present intellectual efficiency", since efficiency would be determined by both factors, not only one. The clinical data indicate that both are of essential importance in intelligence as it would be identified either by tests or by common sense. The contrast is not between intelligence and knowledge, but between capacity to develop new patterns of response and the functioning of those already developed.

Intellectual power might be defined as capacity to develop a test ability in the absence of any previous relevant experience. If a cortical lesion outside the speech areas prevents the acquisition of a normal vocabulary in the developmental period, it should also prevent the same acquisition at maturity, provided the intellectual difficulty at maturity were the same: that is, in a hypothetical individual who had to learn not only the words but also their conceptual basis, the object- and quality-differentiations and complex habit formations common to speech in general. There must be common factors ("identical elements") and transfer of training from one language to another. An individual who had learned one language before receiving a brain injury might learn another more readily than he would have learned it *de novo* after birth injury, although not as well as a normal individual. Without "previous relevant experience" the adult should do no better than the birth-injured, from the assumption that his brain has suffered as much physiological disruption as

the child's. Power to *develop* the ability is therefore diminished by the mature injury, so there is some loss of intellectual power. The level at which the ability, once developed, is retained is not an index of the individual's hypothetical power to develop the ability from scratch: the actual verbal performance is determined not only by this power, but also by the degree of verbal development before the occurrence of the injury.

During development test abilities correlate rather well, justifying the working concept of a general level of ability. In normal growth any test score is an index of this general level. From the age of 20 onward, and after brain injury or schizophrenia, this is less true. Vocabulary is now more nearly an index of a former general level, achieved during development, than of present intellectual power in the sense defined. In this sense, and with the assumptions that have been made, the more sensitive test indices are the better clues to present intellectual power.

But it should also be remembered that many of the abilities needed in ordinary adult life are like vocabulary, a retained level of functioning. For these, the less sensitive indices such as vocabulary will predict level of functioning best, or the Stanford-Binet better than a performance test.

The hypothesis has a bearing on another matter, the development of abilities after birth injury, particularly in those cases which involve a variable degree of dysfunction (revealed by the E.E.G. or by fluctuation of clinical symptoms). Without going into the inferences in detail, these deductions logically follow:

(1) Early lesions will tend to produce low scores in both Binet and performance-test tasks, regarding the Binet as predominantly a level-of-development index, the performance test predominantly as a present-level index.

(2) If the depression of test scores is due to dysfunction more than to the permanent destruction of tissue, reversal or termination of dysfunction will permit a more rapid rise of the performance-test scores, but only a very slow rise of Binet scores. This would be true also when dysfunction is of decreasing severity; in either case one would expect higher performance-test scores than Binet or vocabulary scores. These level-of-development indices would be more stable and less responsive to changes of intellectual efficiency.

(3) When the lesion occurs in the middle of the developmental period, or when dysfunction occurs then or is of increasing severity during growth (as when epilepsy appears late or is becoming worse), the test score pattern would tend to approach that

found in adult deterioration, with Binet and vocabulary indices relatively high.

(4) With sporadic dysfunction (as for example in the variable deterioration of behavior that may be associated with abnormal E. E. G. records), the patient in "good" periods would be better at performance tasks, in bad periods better at Binet tasks.

The hypothesis is based on what appears to be a characteristic difference in the effect of early and late brain injury; but the corollaries of the hypothesis show that the difference need not always be clear-cut. In some cases the effect of early injury might approach that of late injury, and there might be a wide variation of test-score pattern from one case to another. The hypothesis assumes only that certain test scores are less sensitive to adult than to infant injury, and that on the whole there is less disparity in the effect of infant injury on different test scores.

Vocabulary, unsped verbal comprehension and so on may be regarded as primarily indices of a level of past development, while some other tests, more sensitive to the effect of injury to the mature brain, are better indices of "present intellectual power"; keeping in mind, however, the implication of the hypothesis presented—that adult intellectual efficiency in many matters is determined more by the highest past level of intellectual power than by the level of "present intellectual power". There are, in this view, two ways in which a test may function.

Weisenburg and McBride (p. 329) have made a somewhat similar distinction of test material, related to the familiarity or unfamiliarity of the task. Finding no evidence of loss, after right-sided cerebral destruction, in tests of sentence dictation, oral spelling, and vocabulary, they say:

It is noteworthy that these are language tests involving the reproduction of acquired knowledge in situations not unfamiliar to everyday experience. They [the patients] fall furthest below the normal on the Sentence Completion Test, which involves constructive synthetic mental activity in a situation which is not difficult for them to grasp, but still a less natural situation.

Emphasis here should be put on the kind and form of task rather than on "reproduction of acquired knowledge", if this phrase means the reproduction of material in the form in which it was learned. It must be insisted that in an oral vocabulary test the subject is not asked to repeat a form of words as he learned them, and a high score cannot be explained as due to rote memory. In spelling, this is often true; the child in school learns to repeat individual letters in the proper

order; when he is tested as an adult he may make the same response from memory. Vocabulary tests are another matter. Common words are rarely learned by their definitions; still less are the definitions learned by heart. It is their use that is learned. The evidence in Rowe's case, and in Cases 1 and 2 of this paper, shows that comprehension and memory for complex verbal material heard *for the first time* are also insensitive to late injury. The kind of task is familiar; the specific content, and the actual response to be made, are not.

There is a still more cogent reason for not dismissing the vocabulary score of the adult brain-injured as a mere feat of memory. This is the correlation between vocabulary score and post-operative social competence, conversational ability (ability, that is, to understand and communicate ideas) and general level of functioning in ordinary life. I must revert here to the frequency with which relatives or friends, as well as the attending clinicians, report of the patient who has had successful removal of a large amount of cerebral tissue that his intelligence is unimpaired, and the inescapable conclusion that the patient has retained some essential and important part of his intellectual powers. Vocabulary score therefore would be a better index of level of functioning in such matters than test scores which are more sensitive to the effect of brain damage.

INTELLECTUAL CHANGES WITH AGE

The same thing holds true of the intellectual changes of senescence, and it is this that Jones and Conrad (1933) appear to have overlooked in concluding that vocabulary and information scores should not be used in a rating of adult intelligence, on the ground that these scores show no decline with age. As an inference from changes of test-score pattern with age, the distinction they draw is the same that is drawn in this paper: that is, between tests which are more and less susceptible to the effect of injury or atrophy of the brain. But their theoretical interpretation of the facts does not stand closer analysis, nor does the conclusion that some tests measure "basic intelligence", others "acquired abilities". No hard-and-fast line can be drawn between two types of test.

Jones and Conrad conclude that Army Alpha subtests 4 and 8, vocabulary and information, are acquired abilities; and by implication that others are not. No exception need be taken to this if

it meant only that skills developed with experience were more important in some test abilities, or that other tests are more closely related to the physiological status of the cerebrum as it becomes impaired with age. But it is not clear how one can say that vocabulary is an acquired ability while arithmetic or common sense (Test 3) is not. The view is taken that older adults have an unfair advantage with tests of vocabulary and information because they have had a longer time to acquire these things, and that the younger adult has not "enjoyed equal familiarity with the experience variables affecting test score" (p. 249). This argument might have been applied with equal force to other tests. It is not valid if a limited period teaches the subject all he is capable of learning—if inherent capacity, that is, sets a limit to the level attainable. The correlation between information and other tests of intelligence means that the range of knowledge is determined by intellectual capacity as well as by time of exposure to the facts. Deficient experience can certainly lower vocabulary or information scores, but it does not appear that over-experience can greatly raise them in the absence of special motivation. Given a reasonable degree of exposure, score is not a function of amount of further exposure.

In condemning these tests of "acquired information", Jones and Conrad neglect the fact that they may be the best indices, even in senescence, of an important part of intellectual function. Net intellectual efficiency as it is actually manifested certainly does not begin to decline in adolescence, but appears in many occupations to gain steadily up to thirty or forty, and to be well maintained for some time later. The efficiency is not only due to a greater collection of facts, but is manifested often in creative work or in meeting new situations. The manager of a grocery store or bank, the politician, the novelist, the artist, the boat builder and inventor are by no means always most capable in their twenties. If genius often shows up early, it has shown up late as well. Granted that there is an early decline of what Thorndike calls "sheer modifiability" (Thorndike *et al.*, 1928), there is an increase of something else which often more than balances the loss.

The significance of the tests of "acquired information" is greater if they are really indices of important components of adult intelligence. Wechsler (1939, p. 59), who agrees with Jones and Conrad, but not to the extent of rejecting information and vocabulary as tests of intelli-

gence, ascribes continued efficiency in senescence to an increased store of "acquired knowledge". This must be denied. It would be easy to show—tests of information do show it—that older men do not so excel younger men in range of knowledge that a serious loss of intelligence could be hidden. Wechsler's "old clinician" would have a harder time passing factual examinations than the younger one, and still, as Wechsler says, the older man may be the better doctor. If he is, it must be because he is better at solving the problems of medical practice—even if he is not better at solving text-book problems. To rate the intelligence of older men, tests should be used in which they do relatively well, as well as ones in which they do relatively badly.

The implication of the hypothesis presented here is that the formation of the qualitative modifications of behavior may continue for some time after intellectual power has reached its peak, and that when tests of more genuinely adult interest are developed they may be found, unlike "power" tests but like vocabulary and some other tests (Conrad, 1930) to continue to show a rise for some time after the onset of puberty. The functioning of intelligence in practice demands that these subjective products of earlier intellectual activity be available, that the understanding of common situations and the solution of routine problems occur without intellectual effort. The farther this process has gone, the more efficient intelligence will be. No amount of native mathematical aptitude, even to the extent of genius, will make original contributions to higher mathematics possible until the ideas of elementary algebra and geometry are second nature, so that real intellectual effort is saved for the advanced problem. Intellectual development, therefore, involves (A) the development of direct intellectual power, by neural maturation, and (B) the establishment of routine modes of response to common problems, or of perceptual and conceptual modifications leading to qualitative modifications of behavior.

The kind of test ability which is generally thought to reach its peak earliest, perhaps between the ages of 12 to 15 years, is the kind which is also more apt to be sensitive to the effect of brain injury after this period, and sensitive as well to the changes of senescence. Direct intellectual power, therefore, may be thought to be at a maximum before the age of 16 years. What we call intelligence, however, would involve both (A) and

(B). It would therefore continue to rise to the point at which declining intellectual power offset the increase of intellectual products. For some problems, this peak of efficiency would be reached early; for others late, depending on the extent to which subsidiary problems are involved in the solution of the more difficult problems. Pure puzzle-solving might reach its peak early, for each puzzle would be more or less isolated; but insight into social relationships or skill at dealing with other people might reach a peak very much later and then be maintained.⁴ It is granted at once that this high level of problem solving by older subjects is likely to be within a strictly limited range, but this does not justify the psychological conclusion that intelligence begins to decline with adolescence, nor the idea that the older subject gives only an appearance of intelligence. He may not function as well in a wide range of tasks, and may not maintain as high a level of efficiency over long periods; but in all that kind of comprehension which is commonly thought of as demanding maturity of judgment it is likely that the older man has as high a level of functioning as the younger man, if not in many matters a higher one. We have as yet no good measures of "the integrative mental processes interpretative of [adult] experience" (Miles, 1933), but when these processes can be measured one may expect to see a more adequate picture of psychological maturity.

THEORY OF CEREBRAL FUNCTION

If intellectual development in man is of this kind, there are new complications in a field which was complicated enough already: the study of the relationship of intelligence to the human brain.

Recently Lashley (1938) has fundamentally re-oriented the problem by presenting evidence of independent and qualitatively distinct processes making up mammalian intelligence. Discarding a former concept of general intelligence as a single quantitative variable related to total cortical mass, Lashley now takes the position that major differences of intelligence involve qualitative differences in the kind of abstraction possible. Cortical mass is unimportant for some abilities; it is most important for others. For some capacities of the animal the whole cortex may be equipotential, while others may be dependent on a restricted cortical zone. In the analysis of cerebral func-

tion the question becomes: what abilities are localized, and for what abilities must we take into account mass action and equipotentiality of function? Fundamental to this is the difficulty of analyzing human behavior, of isolating the qualitatively distinct functions postulated by Lashley, and it is this difficulty that is made worse by the hypothesis of the present paper.

The clinical evidence reviewed here has been quite in accord with Lashley's position. The apparently generalized effect of infant lesions argues for some degree of equipotentiality of the cortex in development. Even verbal abilities, which seem so sharply localized in the speech areas of the adult, have been seen to be dependent on the integrity of the whole cerebrum for their normal development. The peculiarities and selectivity of the effect of late injury make it clear that the functions comprising normal intelligence must be in some sense independent of one another. It is impossible to predict from deterioration in one ability what others will be involved with it. Attention has been drawn to the anomalous finding of Rylander that differentiation of abstract words is affected by lesions that do not affect total vocabulary. A report has also been given elsewhere (Hebb, 1939) of a case in which a right temporal lobe lesion led to non-verbal behavior like that often found in aphasia, and with apparent disturbances of social comprehension, but without evidence of loss in verbal abilities. These are rather restricted defects which can hardly be arranged in a quantitative series. It was said in discussing Case 2 that such defects cannot be described as the loss of a single intellectual function, and that one ability is never completely lost without others' being affected; but this of course may be due only to the use of tests which measure a *mélange* of functions in varying degree.

It would be most desirable to relate the results of clinical analysis to the pioneering work of Thurstone⁵ (1938, 1940) in the qualitative analysis of "general intelligence" by quantitative methods. The clinical analysis certainly gains support

⁴ And the report by Gilbert (1935) that age has less effect on brighter subjects suggests that net efficiency may rise for a longer period if the original level was high.

⁵ Cattell (1942) in an independent approach to the problem has shown that Spearman's "g" can also be related to this type of analysis. Cattell's theory was developed in part on the basis of the present discussion, but his treatment concerns a wider range of facts and significantly adds to the theory by showing among other things that it makes the "g" hypothesis (with some modification) fit facts from the normal adult and clinical fields which would otherwise appear incompatible with "g".

from his success with the method of simple structure. The re-appearance of the same primary factors in several experiments, with different test batteries and different populations, offers some guarantee that these factors are more than mathematical artefacts. But the variables so found could not be independently measured, even if one attempted to construct tests specially for the purpose; clinical tests are of course even more impure, and it cannot be expected that the loss of a single intellectual function would be detected as loss in a single test ability. This is essentially the reason that there is little evident relation between the results of factor analysis and the crude clinical analysis of test score patterns in deterioration, except in Thurstone's suggestion that amnesic aphasia may be regarded as loss in factor *W*, or "word fluency".

The general significance of Thurstone's results is the same as that of the clinical evidence which points rather obscurely to the functional independence of some of the factors making up human intelligence. On the other hand, the contrast drawn here between the effect of early and late injury to the brain raises the question of how far the clinical suggestion of independent factors may be due to the varying degree to which adult test abilities are related to "present intellectual power" (as the term has been defined). Thurstone and Lashley have raised as a primary problem the question of isolating qualitatively distinct factors in intelligence; the hypothesis presented here adds the problem of distinguishing the direct expression of intellectual power from its effects during growth.

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SUMERIAN LITERATURE; A PRELIMINARY SURVEY OF THE OLDEST LITERATURE IN THE WORLD

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TABLE OF CONTENTS

	PAGE
List of Abbreviations	293
The Significance of Sumerian Literature	293
Inanna's Descent to the Nether World	295
Introduction	295
Transliteration	296
Notes on Transliteration	303
Translation	305
Notes on Translation	312
Excursus A: The Decipherment of Sumerian	316
Excursus B: Sumerian Epics and Myths	318
Plates 1-10	

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LIST OF ABBREVIATIONS

AOF	Archiv für Orientforschung (Berlin).	PBS X 2	Langdon, S. H. <i>Sumerian Liturgical Texts</i> (Philadelphia, 1917).
AS No. 12	Kramer, Samuel N. <i>Lamentation over the Destruction of Ur</i> (Chicago, 1940).	RA	<i>Revue D'Assyriologie et D'Archéologie Orientale</i> (Paris).
BASOR	<i>Bulletin of the American Schools of Oriental Research</i> (Baltimore).	SBH	Reisner, George A. <i>Sumerisch-babylonische Hymnen nach Thontafeln griechischer Zeit</i> (Berlin, 1896).
BE XXXI	Langdon, S. H. <i>Historical and Religious Texts from the Temple Library of Nippur</i> (München, 1914).	SEM	Chiera Edward. <i>Sumerian Epics and Myths</i> (Chicago, 1934).
CBS	Catalogue of the Babylonian Section of the University Museum (followed by number).	SRT	Chiera, Edward. <i>Sumerian Religious Texts</i> (Upland, Pa., 1924).
GSG	Poebel, Arno. <i>Grundsätze der Sumerischen Grammatik</i> (Rostok, 1923).	ŠL	Deimel Anton. <i>Šumerisches Lexicon</i> (Rome, 1930).
HGT	Poebel, Arno. <i>Historical and Grammatical Texts</i> (Philadelphia, 1914).	TRS	Genouillac, Henri de. <i>Textes Religieux Sumeriens du Louvre</i> (Paris, 1930).
JAOS	<i>American Oriental Society, Journal</i> (Boston).	VS II	Zimmern, Heinrich. <i>Sumerische Kultlieder aus altbabylonischer Zeit</i> , 1. Reihe (1912).
K	British Museum. Kouyunjik collection (followed by number).	VS X	Zimmern, Heinrich. <i>Sumerische Kultlieder aus altbabylonischer Zeit</i> , 2. Reihe (1913).
Ni	Museum of the Ancient Orient (Istanbul). Nippur Collection.	ZA	<i>Zeitschrift für Assyriologie und verwandte Gebiete</i> (Leipzig).
PBS I 1	Myhrman, David W. <i>Babylonian Hymns and Prayers</i> (Philadelphia, 1911).		

THE SIGNIFICANCE OF SUMERIAN LITERATURE

THE Sumerians are a non-Semitic people who flourished in southern Babylonia from the beginning of the fourth to the end of the third millennium B.C. During this long stretch of time, the Sumerians, whose racial and linguistic affilia-

tions are still unclassifiable, represented the dominant cultural group of the entire Near East. This cultural dominance manifested itself in three directions:

1. It was the Sumerians who developed and probably invented the cuneiform system of

writing¹ which was adopted by nearly all the peoples of the Near East and without which the cultural progress of western Asia would have been largely impossible.

2. The Sumerians developed religious and spiritual concepts together with a remarkably well integrated pantheon which influenced profoundly all the peoples of the Near East including the Hebrews and Greeks. Moreover, by way of Judaism, Christianity, and Mohammedanism, not a few of these spiritual and religious concepts have permeated the modern civilized world.

3. The Sumerians produced a vast and highly developed literature, largely poetic in character, consisting of epics and myths, hymns and lamentations, proverbs and "words of wisdom." These compositions are inscribed largely in cuneiform script on clay tablets and fragments dated approximately 2000 B.C. In the course of the past hundred years, approximately three thousand such literary pieces have been excavated in the mounds of ancient Sumer. Of this number, *over two thousand*; more than two-thirds of our source material, were excavated by the University of Pennsylvania in the mound covering ancient Nippur in the course of four gruelling campaigns lasting from 1889 to 1900; these Nippur tablets and fragments, therefore, represent the major source for the reconstruction of the Sumerian compositions. As literary products, these Sumerian compositions rank among the finest creations known to civilized man. Their significance for a proper appraisal of the cultural and spiritual development of the Near East can hardly be overestimated. The Assyrians and Babylonians took them over almost in toto. The Hittites translated them into their own language and no doubt imitated them widely. The form and contents of the Hebrew literary creations and to a certain extent even those of the ancient Greeks, were profoundly influenced by them. As practically *the oldest written literature of any significant amount ever uncovered*, it furnishes new, rich, and unexpected source material to the archaeologist and anthropologist, to the ethnologist and student of folk lore, to the students of the history of religion and of the history of literature.

¹For a sketch of the fascinating story of the decipherment of Sumerian, as well as a brief general appraisal of the contents of the Sumerian tablets excavated in the course of the past century, cf. Excursus A: *The Decipherment of Sumerian*.

In spite of their unique and extraordinary significance, and although the large majority of the tablets on which they are inscribed have been excavated almost half a century ago, the translation and interpretation of the Sumerian literary compositions have made relatively little progress to date. The translation of Sumerian is a highly complicated process. The grammar has only comparatively recently been scientifically established, while the lexical problems are still numerous and far from resolved. By far the major obstacle to a trustworthy reconstruction and translation of the compositions, however, is the fact that the greater part of the tablets and fragments on which they are inscribed, and which are now largely located in the Museum of the Ancient Orient at Istanbul and in the University Museum at Philadelphia, have been lying about uncopied and unpublished, and thus unavailable for study. To remedy this situation, I travelled to Istanbul in 1937, and with the aid of a Guggenheim fellowship, devoted some twenty months to the copying of one hundred and seventy tablets and fragments in the Nippur collection of the Museum of the Ancient Orient. And largely with the help of a grant from the American Philosophical Society, the better part of the past two years has been devoted to the studying and copying of the unpublished literary pieces in the Nippur collection of the University Museum. As a consequence we are now already in a position to reconstruct the greater part of the texts of twenty-three unique and significant Sumerian epics and myths and are at last on the very threshold of apprehending their contents.² The completion of the final translation of the epics and myths will be followed by the reconstruction of the contents of the important collection of Sumerian hymns dedicated to their gods and kings. I then hope to concentrate all my time and efforts to the Sumerian lamentations and to their proverbs and wisdom literature; this latter group is particularly difficult to decipher because of the laconic and cryptic wording of their contents. Finally as a crowning achievement it is hoped to reconstruct and translate the Sumerian Tammuz compositions, the forerunners of the ancient myths concerned with the dying god and his resurrection, a group of compositions which are of basic significance for a scientific approach to the history of religion.

²For an outline of the contents of these twenty-three compositions, cf. Excursus B: *Sumerian Epics and Myths*.

As an illustration of the temper and mood, the swing and rythm of Sumerian poetry, may I present to the American Philosophical Society the translation of a myth whose text has been reconstructed and deciphered by me in the course of the past several years. Creatively speaking, it undoubtedly ranks among the great compositions of all times. Its influence on literature has been universal and profound. Moreover the story of its decipherment will furnish an illuminating illustration of the not uninteresting process involved in the reconstruction of a Sumerian literary composition.

INANNA'S DESCENT TO THE NETHER WORLD

Introduction

For many many years, for almost three quarters of a century, a myth usually designated as *Ishtar's Descent to the Nether World* has been known to scholar and layman. Because it is written in Assyrian, a Semitic language, on tablets dating from the first millennium B.C., tablets, therefore, that are later by more than a millennium than our Sumerian literary pieces, it was generally assumed to be of Semitic origin. It is therefore quoted and sited in all major works concerned with mythology and religion as a remarkable example of Semitic myth-making. With the appearance of the publications of the Nippur literary material, however, it gradually became obvious that this "Semitic" myth goes back to a Sumerian original in which Ishtar is replaced by Inanna, her Sumerian counterpart. Arno Poebel, now of the Oriental Institute of the University of Chicago, was the first to locate three small pieces belonging to this myth in the University Museum; these he published under the auspices of the University Museum in 1914. In the very same year, the late Stephen Langdon of Oxford, published two pieces which he had uncovered and copied in the Museum of the Ancient Orient at Istanbul. One of these was the upper half of a large four column tablet, which, as will soon become evident, proved to be of major importance for the reconstruction of our myth. The late Edward Chiera, a member of the faculty of the University of Pennsylvania until called to head the Assyrian Dictionary staff of the Oriental Institute of the University of Chicago, uncovered three additional pieces in the University Museum at Philadelphia. These were published in his two posthumous volumes

of Sumerian literary texts which I prepared for publication by the Oriental Institute in 1934.

By this time, therefore, we had eight pieces, all more or less fragmentary, dealing with the myth. Nevertheless the contents remained obscure, for the breaks were so numerous and came at such crucial points that an intelligent reconstruction of the extant parts of the composition was impossible. It was a fortunate and remarkable discovery of Chiera which saved the situation. He discovered in the University Museum in Philadelphia, the *lower* half of the very same four columns tablet whose *upper* half had been found and copied by Langdon in the Museum of the Ancient Orient in Istanbul years before. The tablet had evidently been broken before or during the excavation and the two halves had become separated, the one was retained in Istanbul and the other came to Philadelphia. Unfortunately, Chiera, who fully recognized the significance of his discovery, died before he was in a position to utilize its contents.

It was by making use of this lower half of the four column tablet, despite the fact, that it, too, is very poorly preserved, that I was enabled to reconstruct the contents of the myth. For when joined to the upper part of the tablet, the combined text furnishes an excellent framework in which and about which all the other texts could be grouped. Needless to say there were still numerous gaps and breaks in the text which made the translation and interpretation of the contents no easy matter, and the meaning of several of the more significant passages remained obscure. In 1937 I was fortunate enough to discover in Istanbul three additional pieces belonging to the myth, and upon returning to the United States in 1939 I located yet another large piece in the University Museum. Quite recently in the process of reexamining the Nippur collection in the University Museum I discovered another small piece which is being published here for the first time. These five pieces helped to fill out the most serious lacunae in my first reconstruction, and as a result, the story, as far as it goes, is now practically complete. It runs as follows:

Inanna, the Queen of Heaven, the goddess of light, and love, and life has set her heart upon visiting the Nether World, perhaps in order to set free her lover Tammuz. She collects all the appropriate divine decrees, adorns herself with her queenly robes and jewels, and is ready to enter the "Land of No Return." Queen of the

Nether World is her elder sister and bitter enemy Ereshkigal, the goddess of darkness, and gloom, and death. Fearing lest her sister put her to death in the Nether World, Inanna instructs her messenger Ninshubur who is always at her beck and call, that if after three days she shall have failed to return, he is to set up a hue and cry for her in Heaven, in the assembly hall of the gods. Moreover, he is to go to Nippur (the very city where our tablets have been excavated) and plead before the great god Enlil to save Inanna from Ereshkigal's clutches. If Enlil refuses, he is to go to Ur (Ur of the Chaldees, whence, according to Biblical tradition, Abraham migrated into Palestine) and plead before Nanna, the great Sumerian moon-god, to come to her rescue. If Nanna, too, refuses, he is to go to Eridu (the city in which Sumerian civilization originated according to Babylonian tradition) and repeat his plea before Enki, the Lord of Wisdom, and the latter, who "knows the food of life," who "knows the water of life," will surely restore her to life.

Inanna then descends to the Nether World and approaches Ereshkigal's temple of lapis lazuli. At the gate she is met by the chief gatekeeper who demands to know who she is and why she has come. Inanna concocts a false excuse for her visit, and the gatekeeper, upon instructions from his mistress leads her through the seven gates of the Nether World. As she passes through each of the gates her garments and jewels are removed piece by piece in spite of her

protests. Finally after entering the last gate she is brought stark naked and on bended knees before Ereshkigal and the Anunnaki, the seven dreaded judges of the Nether World. These fasten upon Inanna their "look of death" and she is turned into a corpse which is then impaled on a stake.

So pass three days and three nights. On the fourth day, Ninshubur, seeing that his mistress has not returned, proceeds to make the rounds of the gods in accordance with his instructions. As Inanna had predicted, both Enlil and Nanna refuse all help. Enki, however, devises a plan to restore her to life. He fashions the *kurgarrû* and the *kalaturru*, two sexless creatures, and he entrusts to them the "food of life" and the "water of life," with instructions to proceed to the Nether World and sprinkle this "food" and this "water" sixty times upon Inanna's impaled corpse. This they do, and Inanna revives. As she leaves the Nether World, however, to re-ascend to the earth, she is accompanied by the dead and by the bogeys and harpies who have their home there. Surrounded by this ghostly, ghastly crowd she wanders from city to city in Sumer.³

³ Here all the extant source material for *Inanna's Descent to the Nether World* unfortunately breaks off. But this is not the end of the myth. It is not too much to hope that some day in the not too distant future, the pieces on which the conclusion of the story is inscribed will be discovered and deciphered.

Transliteration

1. [an-gal]-ta ki-gal-še geštug-ga-ni na-an-g[u b]
2. AN an-gal-ta ki-gal-še geštug-ga-ni na-an-g[u b]
3. ^dinanna an-gal-ta ki-gal-še geštug-ga-ni na-an-g[u b]
4. nin-mu an mu-un-šub ki mu-un-šub kur-ra ba-e-a-e₁₁
5. ^dinanna an mu-un-šub ki mu-un-šub kur-ra ba-e-a-e₁₁
6. nam-en mu-un-šub nam-nin mu-un-šub kur-ra ba-e-a-e₁₁
7. unug^{ki}-ga é-an-na mu-un-šub kur-ra ba-e-a-e₁₁
8. bàd-tibira^{ki}-a é-mùš-kalam-ma mu-un-šub kur-ra ba-e-a-e₁₁
9. zabalām^{ki}-a gi-gu¹⁸^{ki}-na mu-un-šub kur-ra ba-e-a-e₁₁
10. adaba^{ki} é-šar-ra mu-un-šub kur-ra ba-e-a-e₁₁
11. nibru^{ki}-a bara-tuš-gar-ra mu-un-šub kur-ra ba-e-a-e₁₁
12. kiši^{ki}-a ħur-sag-kalam-ma mu-un-šub kur-ra ba-e-a-e₁₁
13. a-ga-dè^{ki} é-ul-maš^{ki} mu-un-šub kur-ra ba-e-a-e₁₁
14. me-imin-bi zag mu-ni-in-kešd
15. me mu-un-kin-kin šu-ni-še mu-un-gál
16. me-DU ġir-gub-ba i-im-DU
17. ^{tú}šū-gur-ra-men-edin-na sag-gá-na mu-un-gál
18. ħi-li sag-ki-na šu ba-ni-in-ti
19. gi-diš-ninda-ŠĒ-gán-za-ġin šu mi-ni-in-du₈

20. ^{na}z a-gìn-tu₁₉-tu₁₉-lá gú-na ba-an-lá
21. ^{na}nunuz-tab-ba gaba-na [ba-ni]-in-si
22. HUR-guškin šu-na ba-ni-in-du₈
23. tu-di-tum-lú-gá-nu-gá-nu gaba-na ba-an-BU
24. ^{tú}palà-a-^{tú}palà-a bar-ra-na ba-an-dul
25. šim(?) -e-ḥé-im-DU-ḥé-im-DU igi-na ba-ni-in-gar
26. ^dinanna kur-šè i-im-du
27. sukkal-a-ni ^dga-ša-an-šubur-ra[zag(?)]-a-na i-im-du
28. kug-^dinanna-ke₄ ^dga-ša-an-šubur-ra gù mu-na-dé-e
29. gi-en-gi-en-mu
30. sukkal-e-ne-è-m-šag₅-šag₅-ga-mu
31. ra-gaba-e-ne-è-m-gi-en-gi-en-na-mu
32. u₄-da kur-šè mu-un-e₁₁-dè
33. u₄-da kur-šè DU-na-mu-dè
34. an du₆-du₆-dam gar-gar-ma-ni-ib
35. èš-gú-en-na tuku-a-ma-ni-ib
36. é-dingir-ri-e-ne-ke₄ nigin-na-ma-ni-ib
37. i-bí-zu HUR-ma-ab ka-zu HUR-ma-ab
38. ki(?) -mu-lu-da u-di-šu-gal-zu HUR-ma-ab
39. mu-lu-nu-tuku-gim túg-aš-a mu₄-ma-ab
40. é-kur-ri-é-^dmu-ul-líl-lá-šè me-ri-zu aš gub-mu-un
41. é-kur-ri-é-^dmu-ul-líl-lá-šè tu-tu-da-zu-dè
42. i-bí-^dmu-ul-líl-lá-šè ír šéš-a
43. a-a-^dmu-ul-líl tu-mu-zu mu-lu kur-ra nam-ba-da-an-gúr-e
44. kug-šag₅-ga-zu saḥar-kur-ra-ka nam-ba-an-da-šár-ri
45. za-gìn-šag₅-ga-zu za-zadim-ma-ka nam-ba-da-an-si-il-li
46. ^{si}urkarin(?) -zu giš-nagar-ra-ka nam-ba-da-dar-dar-ri
47. ki-sikil-^dga-ša-an-na kur-ra nam-ba-da-an-gúr-e
48. u₄-da ^dmu-ul-líl e-ne-è-m-ba nu-ri-gub urí^{ki}-šè DU-na
49. urí^{ki}-é-mud(?) -kalam-ma-ka
50. é-kiš-šir₅-gál-^dnanna-šè tu-tu-da-zu-dè
51. i-bí-^dnanna-šè ír šéš-a
52. a-a-^dnanna tu-mu-zu mu-lu-kur-ra nam-ba-da-an-gúr-e
53. kug-šag₅-ga-zu saḥar-kur-ra-ka nam-ba-an-da-šár-ri
54. za-gìn-šag₅-ga-zu za-zadim-ma-ka nam-ba-da-an-si-il-li
55. ^{si}urkarin(?) -zu giš-nagar-ra-ka nam-ba-da-dar-dar-ri
56. ki-sikil-^dga-ša-an-na kur-ra nam-ba-da-an-gúr-e
57. u₄-da ^dnanna e-ne-è-m-ba nu-ri-gub uru-ši-ib^{ki}-šè DU-na
58. uru-ši-ib^{ki} é-^dam-an-ki-ga-šè tu-tu-da-zu-dè
59. i-bí-^dam-an-ki-ga-šè ír šéš-a
60. a-a-^dam-an-ki tu-mu-zu mu-lu kur-ra nam-ba-da-an-gúr-e
61. kug-šag₅-ga-zu saḥar-kur-ra-ka nam-ba-an-da-šár-ri
62. ^{na}z a-gìn-šag₅-ga-zu za-zadim-ma-ka nam-ba-an-da-si-il-li
63. ^{si}urkarin(?) -zu giš-nagar-ra-ka nam-ba-da-dar-dar-ri
64. ki-sikil-^dga-ša-an-na kur-ra nam-ba-da-an-gúr-e
65. a-a-^dam-an-ki-ù-mu-un-mu-uš-^{si}túg-[da(?)]-ma-al-la-ke₄
66. ú-nam-ti-la mu-un-zu a-nam-ti-la mu-un-zu
67. e-ne ma-ra ḥu-mu-un-ti-li
68. ^dinanna kur-šè i-im-du
69. sukkal-a-ni-^dga-ša-an-šubur-ra gù mu-na-dé-e
70. DU-na ^dga-ša-an-šubur-ra
71. e-ne-a-ra dug₄-ga-mu-? šà la-ba-pàd
72. ^dinanna é-gal-kur-za-gìn-šè um-ma-te
73. ^{si}ig-kur-ra-ka níg-ḥul ba-an-uš

74. é-gal-kur-ra-ka gù-ḥul ba-an-dé
75. é gál-ù i-du₈ é gál-ù
76. é gál-ù ^dNE-ti é gál-ù aš-mu-šè ga-tu
77. ^dNE-ti-i-du₈-gal-kur-ra-ke₄
78. kug-^dinanna-ra mu-un-na-ni-ib-gi₄-gi₄
79. a-ba-me-en-za-e
80. me-e-^dga-ša-an-na ki-^dutu-è-a-aš
81. tukum-bi za-e ^dinanna ki-^dutu-e-a-aš
82. a-na-àm ba-du-un kur-nu-gi₄-šè
83. ḥar-ra-an-lú-du-bi nu-gi₄-gi₄-dè šà-zu a-gim túm-mu-un
84. kug-^dinanna-ke₄ mu-na-ni-ib-gi₄-gi₄
85. nín-gal-mu ^dga-ša-an-ki-gal-la
86. mu dam-a-ni-ù-mu-un-gu₄-gal-an-na ba-an-ug₅-ga
87. ki-si-ga-na i-bí du₈-ù-dè
88. kaš-si-ga-na gu-ùl ba-ni-in-dé hur-šè ḥé-me-a
89. ^dNE-ti-i-du₈-gal-kur-ra-ke₄
90. kug-^dinanna-ke₄ mu-na-ni-ib-gi₄-gi₄
91. túm-túm-ma-ab ^dinanna nin-mà ga-an-na-ab-du₄
92. nin-mu-^dereš-ki-gal-la-ra ga-an-na-du₄... ga-an-na-ab-du₄
93. ^dNE-ti-i-du₈-gal-kur-ra-ke₄
94. nin-a-ni-^dereš-ki-gal-la-ra é-[a-ni-šè ba-a]n-ši-in-tu gù
mu-na-dé-e
95. nin-mu ki-sikil-diš-àm
96. dingir-gim-sukud (?)
97. ^{si}ig
98.
99. é-an-na-ka
100. me imin-bi zag mu-ni-in-kešd
101. me mu-un-kin šu-ni-šè mu-un-gál
102. me-DU gír-gub-ba i-im-DU
103. ^{tú}gu-gur-ra-men-edin-na sag-gá-na mu-un-gál
104. ḥi-li-sag-ki-na šu ba-ni-in-ti
105. gi-diš-ninda-ŠÈ-gán-za-gìn šu mi-ni-in-du₈
106. ^{na}za-gìn-tu₁₉-tu₁₉-lá gú-na ba-an-lá
107. ^{na}nunuz-tab-ba gaba-na ba-ni-in-si
108. HUR-guškin šu-na ba-ni-in-du₈
109. tu-di-tum-lú-gá-nu-gá-nu gaba-na ba-an-BU
110. šim (?) -e-ḥé-im-DU-ḥe-im-DU igi-na ba-ni-in-gar
111. ^{tú}palà-a-^{tú}palà-a bar-ra-na ba-an-dul
112. u₄-ba ^dereš-ki-gal-la-ke₄
113. ^dNE-ti-i-du₈-gal-ni-ir[mu-na-ni-ib-gi₄-gi₄]
114. gá-nu-^dNE-ti i-du₈-[gal-kur-ra]
115. inim (?) -a (?) -ra (?) -du₄ (?) -ga (?) -mu geštug (?)
ḥé (?) -[im (?) -ma (?) -ag (?)]
116. ká-gal-kur-ra imin-bi[^{si}si-gar-bi gál-ù]
117. ká-gal-[ganzir-igi-kur-ra ka-aš-bi bar-ra]
118. e-ne tu-tu-da-ni-ta
119. gam-gam-ma-ni ?-?-nun?-ni-ta
120. ^dNE-ti-i-du₈-gal-kur-ra-[ke₄]
121. inim-nin-a-na-šè sag-kešd ba-ši-[in-ag]
122. ká-gal-kur-ra imin-bi ^{si}si-gar-bi[in-gál]
123. ká-gal-ganzir-igi-kur-ra ka-aš-bi[in-bar]
124. kug-^dinanna-ra gù mu-na-dé-e
125. gá-nu ^dinanna tu-um-[ma-ni]

126. e-ne tu-tu-da-ni-ta
127. ^{túg}u-gur-ra-men-edin-na-sag-gá-na lú ba-da-an-ši-ir
128. ta-àm-me-a
129. diri ^dinanna me-kur-ra-ke₄ šu al-du₇-du₇
130. ^dinanna garza-kur-ra ka-zu na-an-....-e-en
131. ká-gal-min-kam-ma tu-tu-da-ni-ta
132. gi-diš-ninda-ŠĒ-gán-za-gin lú ba-da-an-ši-ir
133. ta-àm-me-a
134. diri ^dinanna me-kur-ra-ke₄ šu al-du₇-du₇
135. ^dinanna garza-kur-ra ka-zu na-an-....-e-en
136. ká-gal-eš-kam-ma tu-tu-da-ni-ta
137. ^{na}za-gin-tu₁₉-tu₁₉-lá-gú-na lú ba-da-an-ši-ir
138. ta-àm-me-a
139. diri ^dinanna me-kur-ra-ke₄ šu al-du₇-du₇
140. ^dinanna garza-kur-ra ka-zu na-an-....-e-en
141. ká-gal-lim-mu-kam-ma tu-tu-da-ni-ta
142. ^{na}nunuz-tab-ba-gaba-na lú ba-da-an-ši-ir
143. ta-àm-me-a
144. diri ^dinanna me-kur-ra-ke₄ šu al-du₇-du₇
145. ^dinanna garza-kur-ra ka-zu na-an-....-e-en
146. ká-gal-ía-kam-ma tu-tu-da-ni-ta
147. HUR-guškin-šu-na lú ba-da-an-ši-ir
148. ta-àm-me-a
149. diri ^dinanna me-kur-ra-ke₄ šu al-du₇-du₇
150. ^dinanna garza-kur-ra ka-zu na-an-....-e-en
151. ká-gal-àš-kam-ma tu-tu-da-ni-ta
152. tu-di-tum-lú-gá-nu-gá-nu-gaba-na lú ba-da-an-ši-ir
153. ta-àm-me-a
154. diri ^dinanna me-kur-ra-ke₄ šu al-du₇-du₇
155. ^dinanna garza-kur-ra ka-zu na-an-....-e-en
156. ká-gal-imin-kam-ma tu-tu-da-ni-ta
157. ^{túg}palà-a-^{túg}palà-a-bar-ra-na lú ba-da-an-ši-ir
158. ta-àm-me-a
159. diri ^dinanna me-kur-ra-ke₄ šu al-du₇-du₇
160. ^dinanna garza-kur-ra ka-zu na-an-....-e-en
161. gam-gam-ma-ni ?-?-nun-?-ni-ta lú.....
162. [kug-^{dereš}]-ki-gal-la-[k]_{e4} ^{ki}gu-za-na i-ni-in-[tuš]
163. ^aa-nun-na-di-kud-imin-bi igi-ni-šè di mu-un-[ši-in-kud]
164. i-bí mu-ši-in-bar i-bí-úš-a-kam
165. [inim]-ma-ne-ne inim-LIPIS-gig-ga-àm
166. ...-tu-ra KA-...-tag(?) -tag-ga-àm
167. [munus]-tu-ra uzu-níg-sìg-šè ba-an-tu
168. uzu-níg-sìg-ga ^{ki}kak-ta lú ba-da-an-lá
169. u₄-eš gi₆-eš um-ta-zal-la-ta
170. sukkal-a-ni-^dnin-šubur-ra-ke₄
171. sukkal-inim-šag₆-šag₆-ga-ni
172. ra-gaba-inim-gi-en-gi-en-na-ni
173. an du₆-du₆-dam mu-un-na-gá-gá
174. èš-gú-en-na mu-un-na-tuku-a
175. é-dingir-ri-e-ne-ke₄ mu-un-na-nigin
176. i-bí-ni mu-un-na-HUR ka-ni mu-un-na-HUR
177. ki(?) -lú-da u-di-šu-gal-ni mu-un-na-HUR
178. mu-lu-nu-tuku-gim túg-aš-a[im-ma]-an-mu₄
179. é-kur-é-^den-líl-lá-šè gir-ni aš mu-un-gub

180. é-kur-é-^den-líl-lá-šè tu-tu-da-ni-ta
 181. igi-^den-líl-lá-šè ír im-ma-šes-šes
 182. a-a-^dmu-ul-líl tu-mu-zu mu-lu kur-ra nam-ba-da-an-gúr-e
 183. kug-šags-ga-zu saḥar-kur-ra-ka nam-ba-an-da-šár-ri
 184. za-gin-šags-ga-zu za-zadim-ma-ka nam-ba-da-an-si-il-li
 185. ^uurkarin(?) -zu giš-nagar-ra-ka nam-ba-dar-dar-ri
 186. ki-sikil-^dga-ša-an-na kur-ra nam-ba-da-an-gúr-e
 187. a-a-^den-líl-li ^dnin-šubur-ra mu-na-ni-ib-gi-gi
 188. dumu-mu an-[gal-la] al bí-in-dug₄ ki-gal-la al bí-in-dug₄
 189. ^dinanna an-[gal-la] al bí-in-dug₄ ki-gal-la al bí-in-dug₄
 190. me-kur-ra me-al-me-al ki-bi-šè sá bí-in-dug₄
 191. a-ba-àm ki-bi-šè(?)? in-na-an-dug₄ al mu(?) -ni-ib-dug₄
 192. a-a-^den-líl inim-ba[nu-na-gub]ur^{ki}-[šè ba]-du-un
 193. ur^{ki} é-mud(?) -kur-ra-ka
 194. é-kiš-šir₅-gál-^dnanna-šè tu-tu-da-ni-ta
 195. igi-^dnanna-šè ír im-ma-šes-šes
 196. a-a-^dnanna tu-mu-zu mu-lu kur-ra nam-ba-da-an-gúr-e
 197. kug-šags-ga-zu saḥar-kur-ra-ka nam-ba-an-da-šár-ri
 198. za-gin-šags-ga-zu za-zadim-ma-ka nam-ba-da-an-si-il-li
 199. ^uurkarin(?) -zu giš-nam-nagar-ra-ka nam-ba-dar-dar-ri
 200. ki-sikil-^dga-ša-an-na kur-ra nam-ba-da-an-gúr-e
 201. a-a-^dnanna ^dnin-šubur-ra mu-na-ni-ib-gi-gi
 202. dumu-mu an-[gal-la] al bí-in-dug₄ ki-gal-la al bí-in-dug₄
 203. ^dinanna an-[gal-la] al bí-in-dug₄ ki-gal-la al bí-in-dug₄
 204. me-kur-ra me-al-me-al ki-bi-šè sá bí-in-dug₄
 205. a-ba-àm ki-bi-šè(?)? in-na-an-dug₄ al mu(?) -ni-ib-dug₄
 206. a-a-^dnanna inim-ba[nu-na-gub]uru-ši-ib^{ki}-šè ba-du-un
 207. uru-ši-ib^{ki} é-^den-ki-ga-šè tu-tu-da-ni-ta
 208. igi-^den-ki-ga-šè ír im-ma-šes-šes
 209. a-a-^dam-an-ki tu-mu-zu mu-lu kur-ra nam-ba-da-an-gúr-e
 210. kug-šags-ga-zu saḥar-kur-ra-ka nam-ba-an-da-šár-ri
 211. za-gin-šags-ga-zu za-zadim-ma-ka nam-ba-da-an-si-il-li
 212. ^uurkarin(?) -zu giš-nagar-ra-ka nam-ba-dar-dar-ri
 213. ki-sikil-^dga-ša-an-na kur-ra nam-ba-da-an-gúr-e
 214. a-a-^den-ki ^dnin-šubur-ra-ke₄ mu-un-na-ni-ib-gi-gi
 215. dumu-mu a-na bí-in-ag mà-e mu-un-kúš-ù
 216. ^dinanna-ke₄ a-na bí-in-ag mà-e mu-un-kúš-ù
 217. nin-kur-kur-r[a-ke₄]a-na bí-in-ag mà-e mu-un-kúš-ù
 218. nu-u₈-gig-an-na-ke₄ a-na bí-in-ag mà-e mu-un-kúš-ù
 219. ?-?-ni mu-sír ba-ra-an-túm kur-gar-ra ba-an-dím
 220. ?-dirig?-ma-na mu-sír ba-ra-an-túm ga[la-tur ba-an]-dím
 221. kur-gar-ra ú-nam-ti-la ba-an-[si(?)]
 222. kala-tur-ra a-nam-ti-la ba-an-[si(?)]
 223. [a-a]-^den-ki kala-tur-kur-gar-ra gù mu-u[n-ne-dé-e]
 224.-an-ši-en GĪR-kur-TÚG ná-ba-an-ši-en
 225.-a.....-dè-en-si-en
 226.-dè-en-si-en
 227.-šè
 228.-ra-àm
 229.
 230.
 231.-ni
 232.-na-....-eš
 233.-ni

234. dug₄(?) - ga - na - ab - ši - en
 235. - ši - en
 236. - mu (?) - ta (?) KA ba - e - dè - en - ši - en
 237. dug₄(?) - ga (?) en (?) ši - en
 238. ib (?) - tar (?) - ri (?) - en - ši - en
 239. - dè - en - ši - en
 240. a - a - ab - ši - en
 241. a - a - na (?) kug (?) - e - dè šu nam - ba - bu - i - en - ši - en
 242. a - ? - tu (?) - na (?) kug - e - dè šu nam - ba - bu - i - en - ši - en
 243. uzu - níg - sig - ga - ^{si}kak - ta - lá - a ní - me - lám dug₄ - ga - na - ab - ši - en
 244. gíš - àm ú - nam - ti - la gíš - àm a - nam - ti - la ugu - na
 šub - bu - dè - en - ši - en
 245. ^dinanna ha - ba - gub
 Break of 20(?) lines.
 266. ^{si}kak - ta
 267. kug - ^dereš - ki - gal - la - la - ke₄ ka [la - tur - kur - gar - ra
 mu - ne - ni - ib - gi₄ - gi₄]
 268. uzu - àm - sig me - àm ga (?)
 269. uzu - níg - giš (?) - ra (?) - a ÁG (?) - húl (?) - la ? me (?) - teš (?)
 in - na - [an - dug₄ - gi - eš]
 270. uzu - níg - sig ^{si}kak - ta - lá - a ní - me - lám (?) ? - uš
 271. gíš ú - nam - ti - la gíš a - nam - ti - la ugu - na bí - in - šub - bu - uš
 272. ^dinanna ba - gub
 273. ^dinanna kur - ta ba - e₁₁ - dè
 274. ^da - nun - na - ke₄ - ne ba - ab - zaḥ - aš
 275. a - ba - àm - lú - kur - ra - ke₄ - ne kur - ra silim - ma - bi e₁₁ - dè
 276. u₄ - da ^dinanna kur - ta ba - e₁₁ - dè
 277. ug₅ - ga sag - a - na ha - ba - ab - si - mu
 278. ^dinanna kur - ta ba - e₁₁ - dè
 279. galla - tur - tur gi - igi - dū - ra (?) - gim
 280. galla - gal - gal gi - dub - ba - na - ke₄
 281. zag - ga - na ba - an - dib - bi - eš
 282. lú - igi - na - dib - nu - me - a gišdar šu bi - in - du₅
 283. bar - ra - na - dib - nu - me - a ^{si}tukul úr - ra bí - in - lá
 284. lú - e - ne - ra - in - ši - sùg - eš - àm
 285. lú - ^dinanna - ra - in - ši - sùg - eš - àm
 286. ú - nu - zu - me - eš a - nu - zu - me - eš
 287. zi - dub - dub - ba - nu - kú - me - eš
 288. [kaš (?)] - bal - bal nu - nag - nag - me - eš
 289. úr - lú - ka dam šu - ti - a - me - eš
 290. ? - umme - da - lá - ka dumu - šu - ti - a - me - eš
 291. ^dinanna kur - ta ba - e₁₁ - dè
 292. ^dinanna kur - ta e₁₁ - da - ni
 293. [sukkal - a - ni] ^dnin - šubur - ke₄ gir - ni - šè ba - an - šub
 294. saḥar - ra ba - da - an - tuš ^{is}mu - sír - ra ba - an - mu₄
 295. galla - e - ne kug - ^dinanna - ra gù mu - un - na - dé - e
 296. ^dinanna uru - zu - šè gub - ba e - ne ga - ba - ab - túm - mu - dè
 297. kug - ^dinanna - ke₄ galla - e - ne mu - na - ni - ib - gi₄ - gi₄
 298. sukkal - e - ne - èm - šag₅ - šag₅ - ga - mu
 299. ra - gaba - e - ne - èm - gi - en - gi - na - mu
 300. na - ri - ga - mu šu nu - mu - un - bar - ri
 301. e - ne - èm - dug₄ - ga - mu gú - zal la - ba - pàd
 302. an dū₆ - du₆ - da ma - an - gá - gá
 303. èš - gú - en - na ma - an - tuku - a

304. é-dingir-ri-e-ne-ke₄ ma-an-nigin
 305. i-bí-ni ma-an-ĤUR ka-ni ma-an-ĤUR
 306. ki(?) - mu-lu-da u-di-šu-gal-a-ni ma-an-ĤUR
 307. mu-lu-nu-tuku-gim túg-aš-a im-ma-an-mu₄
 308. é-kur-ra-é-^dmu-ul-líl-lá-šè
 309. ur^{ki}-ma é-^dnanna-šè
 310. uru-ši-ib^{ki} é-^dam-an-ki-ga-šè
 311. e-ne ma-a-ra mu-un-ti-li-en
 312. ga-an-ši-súg-dè-en umma^{ki}-a sig₄-kur-šà-ga-šè
 ga-an-ši-súg-dè-en
 313. umma^{ki}-a sig₄-kur-šà-ga-ta
 314. ^dšara gír-ni-šè ba-an-šub
 315. saḥar-ra ba-da-an-tuš ^{tú}mu-sír-ra ba-an-mu₄
 316. galla-e-ne kug-^dinanna-ra gù mu-na-dé-e
 317. ^dinanna uru-zu-šè gub-ba e-ne ga-ba-ab-túm-mu-dè
 318. kug-^dinanna-ke₄ galla-e-ne mu-na-ni-ib-gi₄-gi₄
 319. ià(?) - giš(?) - máš(?) - gud(?)
 320. ? gú-TAR-lá
 321. NE-ta gim-nam ḥ[i(?) - l]i(?) - aš(?) ši-è m(?)
 322. ga-e-súg-en-dè-en bād-tibira^{ki}-a é-mùš-kalam-ma-šè
 ga-an-ši-súg-en-dè-en
 323. bād-tibira^{ki}-a é-mùš-kalam-ma-ta
 324. ^d..... -e gír-ni-šè ba-an-šub
 325. saḥar-ra ba-da-an-tuš ^{tú}mu-sír-ra ba-an-mu₄
 326. galla-e-ne kug-^dinanna-ra gù mu-na-dé-e
 327. ^dinanna uru-zu-šè gub-ba e-ne ga-ba-ab-túm-mu-dè
 328. kug-^dinanna-ke₄ galla-e-ne mu-un-na-ni-ib-gi₄-gi₄
 329. á-zi-da-gùb-bu-mu-uš
 330. -ib-ši-è m
 331. -la ga-sì kul-aba^{ki}] - ...
 332. kul-aba^{ki}-a
 333. AN
 Break of 40(?) lines.
 374.
 375. kur-kur-ra
 376. NE(?) ki(?) - tuš(?) - bi
 377. šub(?) - šub(?) - ba mu-un-ri-eš
 378. -ni i-in-sig-gi-ne
 379. e(?) - ne i-lu mi-ni-ib-bi-ne
 380. -e ? - ni bí-in-šub-bu-uš
 381. gú(?) - giš dùg(?) súg(?) - súg(?) - e-dè
 382. šu-ni mi-ni-in-dù-dù
 383. -kur-kur-ra igi mi-ni-ib-fl-fl-i
 384. -ne-ne -ga(?) - me-eš me-luḥ(?) ? kal-la-mu

Notes on the Transliteration

The texts on which the reconstruction of our myth is based are as follows:

Lines	1-208	A (= Ni 368 + CBS 9800) i-iv
	1-49	B (= CBS 13932) obv. and rev.
	1-48	C (= CBS 12368 + 12702 + 12752) obv. and rev.
	3-25	D (= Ni 2279) obv. (rev. destroyed)
	52-95	E (= CBS 13908) obv. and rev.
	88-94	F (= Ni 4034) obv. (rev. destroyed)
	95-141	G (= CBS 11064 + 11088) obv. and rev.
	129-137	H (= HGT No. 24)
	144-204	I (= CBS 15212) obv. and rev.
	207-244	J (= Ni 4200) obv. and rev.
	225-242	K (= Ni 2762) obv.
	265-323	L (= CBS 13902) obv. and rev.
	273-295	K rev.
	302-313	M (= CBS 15162) obv.
	354-364	M rev.

The upper half of A (*cf.* Pls. 1 and 2), Ni 368, is in the Museum of the Ancient Orient at Istanbul. It was first published by Langdon in BE XXXI No. 33 and then republished by Chiera in SRT No. 53 (for corrections to the latter, *cf.* Kramer, RA XXXVI pp. 76-80). The lower half of A, CBS 9800, is in the University Museum at Philadelphia. It was first published by me in photographic form in RA XXIV p. 93 ff. B and C (*cf.* Pls. 3 and 4) have been published by Chiera in SEM Nos. 49 and 50. D has been published by Langdon in BE XXXI No. 34 (for corrections, *cf.* Kramer, JAOS 60 p. 246). In the case of E (*cf.* Pl. 5), its reverse only has been published by Chiera in SEM No. 48. F (*cf.* Pl. 10) was copied by me in the Museum of the Ancient Orient at Istanbul. G (*cf.* Pl. 6) has been published by Poebel in HGT No. 23 (*cf.* also *ibid.* Pl. XCIV). H has been published by Poebel in HGT No. 24. I (*cf.* Pl. 7) has been published by me in BASOR No. 79 p. 18ff. J and K (*cf.* Pl. 8) have been published by me in RA XXXVI p. 68ff. L (*cf.* Pl. 9) has been published by Poebel in HGT No. 22. M (*cf.* Pl. 10) has been discovered and copied by me recently in the University Museum at Philadelphia.

The reconstruction of the myth *Inannas' Descent to the Nether World* together with the transliteration and translation as presented in this study is intended to supersede that published by me in RA XXXIV pp. 93-134, RA XXXVI pp. 68-80, and BASOR No. 79 pp. 18-27.

Line 1.—For omission in SRT 53, *cf.* RA XXXVI p. 76.

Line 3.—In D the second sign is Inanna, not NUN.

Line 4.—D omits the -e- of ba-e-a-e₁₁ in this and the following lines.

Lines 7-13.—A omits the refrain kur-ra ba-e-a-e₁₁ in these lines. In B the list of cities and temples is identical with that of A, only the order varies; thus: Uruk, Zabalam, Adab, Agade, Kish, Badtibira, Nippur (*cf.* RA XXXVI pp. 76-7). In line 9, B actually has -ga for the expected -na in gi-gu₁₅^{ki}-na; this is probably a scribal error. In line 13, B adds -a after a-ga-dè^{ki} and also after é-ul-maš^{ki}. C lists only two cities and temples; the names are destroyed.

Line 15.—B has -u₈- for -un- in mu-un-gál; in C the verb reads [mu]-un-gar.

Line 16.—D has -D Û G for -DU in me-DU; in D the verb reads u-m-mi-in-[DU].

Lines 17-25.—The order of these lines is based on A; in B the order is: 17, 18, 21, 20, 23, 24, 25, 19, 22 (the latter line is destroyed); in C the order is: 17, 18, 23, 24, 22, 20, 21, 15, 19; in D the order is: 17, 18, 24, 23, 22, 20, 21 (19 and 25 are destroyed). In line 18, B omits the -na of sa-gá-na. Note the corrected reading of line 19, the sign following -ŠÈ- is GĀN (not GĀ); *cf.* the erroneous reading in RA XXXIV p. 99 (especially note 9); *cf.* also BASOR No. 79 p. 24, note 9. For šu-mi-ni-in-du₈ of this line C has šu-na-ba-an-du₈. In line 20, not only D but also A and C have -lā after -tu₁₉-tu₁₉ (Chiera's copies are to be corrected accordingly), only B omits the -lā. In line 21, the verb reads ba-an-si in B and C; in B the sign copied by Chiera as GIM is BA written over an erasure. In C the verbal form of line 22 reads ba-an-du₈. In line 23 note that A seems to insert a sign after the ga ba of ga ba-na; *cf.* BASOR No. 79 p. 24, especially note 8. In line 24, A omits the -a after the first palā-; D omits the determinative before the second -palā-; C, no doubt as the result of a scribal error, actually has bar-bi for the expected bar-ra-na.

* The break in M between the last line of its obverse and the first line of its reverse is assumed to contain 40 lines.

Note that the last sign in this line is DUL (*i.e.* ROEC 542) and SRT 53 is to be corrected accordingly; *cf.* RA XXXVI p. 77. In line 25, C has -ni for the -na of *igi-na*, and -ib- for the -in- of *ba-ni-in-gar*.

Lines 26-27.—Both lines are omitted in C.

Line 28.—C has the expected *nin-* for *ga-ša-an-*.

Lines 29-31.—In C, line 29 reads: [gá-nu sukkal]-zi-é-an-na-mu; in line 31, C omits the -en- of -en-na-mu. B has a variant reading for ll. 29-31, as follows:

[gá-n]u sukkal-zi-é-an-na-mu
[na] ga-e-ri na-ri-mu hē-[dīb]
[inim] ga-ra-ab-dug₄ geštug X⁵
hē-[im-ma-ag]

Line 32.—In C the verb reads *e₁₁-dè-en*; it lacks the expected prefix.

Line 33.—In C the verb reads *e₁₁-dè-mu-dè*.

Lines 34-40.—In lines 34, 35, 36, and 40, B has the indicative forms *mu-un-na-gá-gá*, *mu-un-na-tuku-a*, *mu-un-na-nigin*, and *mu-un-[gub]* instead of the imperative forms; these variants are no doubt the result of a scribal error. In line 40, C seems to have a verbal form ending in -na instead of the expected *gub-mu-un*.

Line 42.—B has *IGI-* for *i-bí-*, and -àm for -a.

Lines 43-47.—In line 44, B has -da-ab- for -an-da- in the verb. In l. 45, B omits the -ma- after -zadim-; it reads -si-il-si-il for -si-il-li in the verb; C has -ab- for -an- in the verb. In line 46, A inserts -nam between *giš-* and -nagar- (also in lines 55, 63).⁶ The verb in line 46 probably reads *nam-ba-da-dar-dar-ri* in A; in B and probably in C, it reads *nam-ba-an-dar-dar-e*.

Line 48.—C inserts -mu-e- before the -ri- of *nu-ri-gub*.

Line 50.—B has -kur-ra- for -kalam-ma-.

Line 55.—E has -si-il-si-il for -si-il-li.

Line 59.—E has -àm for -a after -šéš-.

Line 62.—E omits the determinative *na*, and has -si-il-si-il for -si-il-li.

Line 67.—E probably inserts -a- after the *ma-* of *ma-ra*, and probably omits the *hu-* of the verb. A adds -en after -li-.

Lines 68-69.—Between these two lines E inserts a line reading:

sukkal-a-ni-^dnin-šubur-ra
[zag(?)]-a-na i-im-DU

Cf. line 27.

Line 74.—Line omitted in E.

Lines 75-76.—In E these two lines are written as three, thus:

é gál-lu i-[du₈ é gál-lu]
i-du₈ é gál-lu ^d[NE-ti é gál-lu]
i-du₈ é gál-lu aš-mu-šè ga-tu

Line 78.—E has -ke₁ for -ra (scribal error) and omits the -un- of the verb.

Line 80.—E inserts -an- between -an- and -na; B has -šè for -aš.

Line 81.—E has an-na for ^dinanna.

Line 82.—E omits -àm.

Line 83.—E inserts -ù- between -du- and -bi-.

Line 90.—F inserts -un- after *mu-* in the verb.

Line 94.—F has -šè for -ra after -la-.

Lines 100-111.—For restoration, *cf.* lines 14-25. Note that A is inconsistent in the order arrangement of lines 24-25 and the corresponding lines 110-111. In G, the order of the lines varied from that of A, but the surface is too badly broken for a detailed account.

Line 117.—For the restoration of the line, *cf.* line 123 which is based on G. In A, the line seems to read:

ká-gal-IGI.ZA.KUR...kur-
ra(?)

In G, too, the traces do not point to the same reading of the line as that restored from line 123.

Line 118.—Restorations that are quite certain because of continued repetitions are not bracketed.

Lines 126-127.—In line 126, G has ^dinanna for e-ne. Instead of line 127, G substitutes the text of line 132, and follows it by two lines reading:

ká-gal-diš-kam-ma-tu-tu-da-ni-ta
¹⁰gu-gur-ra-men-edin-na-sag-
gá-na lú ba-da-an-ši-ir

Line 132.—In G the line reads:

hi-li-sag-ki-na lú ba-da-an-ši-ir

⁵ For the form of the sign, *cf.* SRT No. 6 obv. 27-8, and TRS No. 22, line 8.

⁶ So also in line 55; in l. 63, however, A inserts -an- between -da- and -dar-.

Line 137.—In G the line reads:

^{na}nunuz-tab-ba-zag-ga-na lú
ba-da-an-ši-ir

Line 142.—I substitutes the text of line 157.

Line 157.—I substitutes the text of line 132.

Line 161.—Cf. line 119.

Line 163.—SRT No. 53 iii 22 is to be corrected accordingly.

Line 166.—This line is omitted in I.

Line 168.—I omits the -ga after -sig-; it has -an-ta- for -da-an- in the verb.

Line 169.—I has àm- for um-ta- in the verb.

Line 171.—A has the Emesal form -e-ne-è m- for -inim-.

Line 172.—A has the Emesal form -e-ne-è m- for -inim-; I omits the -en- of -en-na-ni and has -mu for -ni (scribal error). Following line 172, I inserts two additional lines:

[na]-ri-ga-ni šu nu-bar-ri
[inim]-dug-ga-ni gú-zal la-ba-pàd

Line 178.—A probably has -ab- for -an- in the verb.

Line 179.—I has the Emesal form -mu-ul-líl- for -en-líl-.

Line 180.—I has the Emesal form -mu-ul-líl- for -en-líl-. For tu-tu-da-ni-ta, A seems to have a variant reading which is illegible.

Line 183.—In A the last sign is -e instead of -ri.

Line 184.—I omits -ma- after -zadim-, and has -si-il-si-il for -si-il-li.

Line 185.—In I the last sign is -e instead of -ri.

Lines 188-191.—For restoration of this passage and that of lines 202-205, cf. RA XXXVI pp. 79-80 and BASOR No. 79, p. 27. Note that in line 190, there is probably nothing missing after bí-in-dug₄. In line 191, the transliteration assumes that there is nothing missing between in-na-an-dug₄ and al.

Line 193.—Note that A writes -kur-ra- in this line although it writes -kalam-ma- in the corresponding line 49.

Lines 202-205.—Cf. lines 188-191.

Line 209.—Note that in J, the traces of the sign preceding -zu do not point to its restoration as -mu (of the expected tu-mu-zu); perhaps the scribe wrote the e-me-KU dumu instead.

Line 211.—J omits the -ma- after -zadim-.

Line 213.—J inserts -an- between -an- and -na.

Line 234.—In K the corresponding line seems to end in -eš.

Line 245.—For the size of the break following line 245, cf. RA XXXVI p. 74, note 3.

Line 279.—In K the corresponding line is rev. 16.

Lines 280-281.—In K, rev. 17 corresponds to these two lines. Note that K probably has -ka for -ke₄ in gi-dub-ba-na-ke₄. The verbal form, too, which is badly broken in K, probably varied.

Line 283.—L has mu-un- for bí-in-.

Lines 284-285.—Both lines are omitted in K.

Line 287.—K inserts ù after -kú-.

Line 288.—Between lines 288 and 289, K inserts a line which reads:

..... [š u n u] -
b u - i - m e - e š

Line 290.—Following this line, K inserts two lines which read:

..... u r n u - z u (?)
..... [m u] - u n -
u r₄ - u r₄ - r i - e š

Line 291.—K omits this line.

Line 302.—M omits -en- in the first complex, and -a after b à d - t i b i r a^{k1}; it probably omits the final complex ga-an-ši-i-súg-en-de-en.

Translation

1. From the ["Great Above"] she set her mind towards the "Great Below",
2. The goddess, from the "Great Above" she set her mind towards the "Great Below",
3. Inanna, from the "Great Above" she set her mind towards the "Great Below".
4. My Lady abandoned Heaven, abandoned Earth, to the Nether World she descended,
5. Inanna abandoned Heaven, abandoned Earth, to the Nether World she descended,
6. Lordship she abandoned, Ladyship she abandoned, to the Nether World she descended.

7. In Uruk she abandoned Eanna, to the Nether World she descended,
8. In Badtibira she abandoned Emushkalamma, to the Nether World she descended,
9. In Zabalam she abandoned Giguna, to the Nether World she descended,
10. In Adab she abandoned Esharra, to the Nether World she descended,
11. In Nippur she abandoned Baratushgarra, to the Nether World she descended,
12. In Kish she abandoned Hursagkalamma, to the Nether World she descended,
13. In Agade she abandoned Eulmash, to the Nether World she descended.
14. The seven decrees she fastened at the side,
15. She sought out the decrees, placed them at her hand,
16. *All the decrees she set up at (her) waiting foot,*
17. The Shugurra, the crown of the plain, she put upon her head,
18. *Radiance* she placed upon her countenance,
19. The rod of lapis lazuli she gripped in (her) hand,
20. Small lapis lazuli stones she tied about her neck,
21. *Sparkling* stones she fastened to her breast,
22. A gold ring she gripped in her hand,
23. A breastplate she bound about her breast,
24. All the garments of Ladyship she *arranged* about her body,
25. *herbs* she put on her face.
26. Inanna walked towards the Nether World,
27. Her messenger Ninshubur walked at her [*side*].
28. The pure Inanna says to Ninshubur:
29. "Oh (thou who art) my constant support,
30. My messenger of favorable words,
31. My carrier of supporting words,
32. I am now descending to the Nether World.
33. When I shall have come to the Nether World,
34. *Fill Heaven with complaints for me,*
35. In the assembly shrine *cry out* for me,
36. In the house of the gods *rush about* for me,
37. *Lower* thy eye for me, *lower* thy mouth for me,
38. With *lower* thy great for me,
39. Like a pauper in a single garment dress for me,
40. To the Ekur, the house of Enlil, direct thy step.
41. Upon thy entering the Ekur, the house of Enlil,
42. Weep before Enlil:
43. 'Oh Father Enlil, let not thy daughter be *put to death* in the Nether World,
44. Let not thy good metal be *ground up* into the dust of the Nether World,
45. Let not thy good lapis lazuli be *broken up* into the stone of the stone-worker,
46. Let not thy *boxwood* be *cut up* into the wood of the wood-worker,
47. Let not the maid Inanna be *put to death* in the Nether World.'
48. If Enlil does not stand by thee in this matter, go to Ur.
49. *In* Ur upon thy entering the house of the of the Land,
50. The Ekishshirgal, the house of Nanna,
51. Weep before Nanna:
52. 'Oh Father Nanna, let not thy daughter be *put to death* in the Nether World,
53. Let not thy good metal be *ground up* into the dust of the Nether World,
54. Let not thy good lapis lazuli be *broken up* into the stone of the stone-worker,
55. Let not thy *boxwood* be *cut up* into the wood of the wood-worker,
56. Let not the maid Inanna be *put to death* in the Nether World.'

57. If Nanna does not stand by thee in this matter, go to Eridu.
58. *In* Eridu, upon thy entering the house of Enki,
59. Weep before Enki:
60. 'Oh Father Enki, let not thy daughter be *put to death* in the Nether World,
61. Let not thy good metal be *ground up* into the dust of the Nether World,
62. Let not thy good lapis lazuli be *broken up* into the stone of the stone-worker,
63. Let not thy *boxwood* be *cut up* into the wood of the wood-worker,
64. Let not the maid Inanna be *put to death* in the Nether World.'
65. Father Enki, the Lord of Wisdom,
66. Who knows the food of life, who knows the water of life,
67. He will surely bring me to life."

68. Inanna walked towards the Nether World,
69. To her messenger Ninshubur she says:
70. "Go, Ninshubur,
71. *The word* which I have commanded thee"

72. When Inanna had arrived at the lapis lazuli palace of the Nether World,
73. At the door of the Nether World she *acted* evilly,
74. In the palace of the Nether World she spoke evilly:
75. "Open the house, gatekeeper, open the house,
76. Open the house, Neti, open the house, all alone I would enter."

77. Neti, the chief gatekeeper of the Nether World,
78. Answers the pure Inanna:
79. "Who, pray, art thou?"

80. "I am the Queen of Heaven, the place where the sun rises."

81. "If thou art the Queen of Heaven, the place where the sun rises,
82. Why, pray, hast thou come to the Land of No Return,
83. How has thy heart led thee on the road whose traveller returns not?"

84. The pure Inanna answers him:
85. "My elder sister, Ereshkigal,
86. Because her husband, the lord Gugalanna, had been killed,
87. To witness his funeral rites,
88. ; so be it."

89. *Neti*, the chief gatekeeper of the Nether World,
90. Answers the pure Inanna:
91. "*Stay*, Inanna, to my queen let me speak,
92. To my queen Ereshkigal let me speak . . . let me speak."

93. *Neti*, the chief gatekeeper of the Nether World,
94. Enters the [house] of his queen Ereshkigal (and) says to her:
95. "Oh my queen, a maid,
96. Like a god
97. The door
98.
99. In Eanna
100. The seven decrees she has fastened at the side,
101. She has sought out the decrees, has placed them at her hand,
102. *All the decrees she has set up at (her) waiting foot*,
103. The Shugurra, the crown of the plain, she has put upon her head,

104. *Radiance* she has placed upon her countenance,
105. The rod of lapis lazuli she has gripped in (her) hand,
106. Small lapis lazuli stones she has tied about her neck,
107. *Sparkling* stones she has fastened to her breast,
108. A gold ring she has gripped in her hand,
109. A breastplate she has bound about her breast,
110. *herbs* she has put on her face,
111. All the garments of Ladyship she has *arranged* about her body."

112. Then Ereshkigal,
113. [Answers] *Neti*, her chief gatekeeper:
114. "Come, *Neti*, [chief] gatekeeper of the [Nether World],
115. *Unto the word which I command thee*, [give ear].
116. Of the seven gates of the Nether World, [open their locks],
117. Of the gate [Ganzir, the face of the Nether World, define its rules].
118. Upon her entering,
119. Bowed low let her"

120. *Neti*, the chief gatekeeper of the Nether World,
121. Honored the word of his queen.
122. Of the seven gates of the Nether World, [he opened] their locks,
123. Of the gate, Ganzir, the face of the Nether World, [he defined] its rules.
124. To the pure Inanna he says:
125. "Come, Inanna, enter."

126. Upon her entering,
127. The Shugurra, the crown of the plain of her head was removed.
128. "*What, pray, is this?*"
129. "Extraordinarily, Oh Inanna, have the decrees of the Nether World been perfected,
130. Oh Inanna, *do not question* the rites of the Nether World."

131. Upon her entering the second gate,
132. The rod of lapis lazuli was removed.
133. "*What, pray, is this?*"
134. "Extraordinarily, Oh Inanna, have the decrees of the Nether World been perfected,
135. Oh Inanna, *do not question* the rites of the Nether World."

136. Upon her entering the third gate,
137. The small lapis lazuli stones of her neck were removed.
138. "*What, pray, is this?*"
139. "Extraordinarily, Oh Inanna, have the decrees of the Nether World been perfected,
140. Oh Inanna, *do not question* the rites of the Nether World."

141. Upon her entering the fourth gate,
142. The *sparkling* stones of her breast were removed.
143. "*What, pray, is this?*"
144. "Extraordinarily, Oh Inanna, have the decrees of the Nether World been perfected,
145. Oh Inanna, *do not question* the rites of the Nether World."

146. Upon her entering the fifth gate,
147. The gold ring of her hand was removed.
148. "*What, pray, is this?*"
149. "Extraordinarily, Oh Inanna, have the decrees of the Nether World been perfected,
150. Oh Inanna, *do not question* the rites of the Nether World."

151. Upon her entering the sixth gate.
152. The breastplate of her breast was removed.
153. "What, pray, is this?"
154. "Extraordinarily, Oh Inanna, have the decrees of the Nether World been perfected,
155. Oh Inanna, *do not question* the rites of the Nether World."
156. Upon her entering the seventh gate,
157. All the garments of Ladyship of her body were removed.
158. "What, pray, is this?"
159. "Extraordinarily, Oh Inanna, have the decrees of the Nether World been perfected,
160. Oh Inanna, *do not question*, the rites of the Nether World."
161. Bowed low
162. [The pure Eresh]kigal [seated] herself upon her throne,
163. The Anunnaki, the seven judges, [pronounced] judgment before her,
164. They fastened (their) eyes upon her, the eyes of death.
165. *At* their [word], the word which tortures the spirit,
166.
167. *The sick* ["woman"] was turned into a *corpse*,
168. The *corpse* was hung from a *stake*.
169. After three days and three nights had passed,
170. Her messenger Ninshubur,
171. Her messenger of favorable words,
172. Her carrier of supporting words,
173. *Fills* the Heaven *with complaints* for her
174. *Cried out* for her in the assembly shrine,
175. *Rushed about* for her in the house of the gods,
176. *Lowered* his eye for her, *lowered* his mouth for her,
177. *With* he *lowered* his great for her,
178. Like a pauper in a single garment he dressed for her,
179. To the Ekur, the house of Enlil, he directed his step.
180. Upon his entering the Ekur, the house of Enlil,
181. Before Enlil he weeps:
182. "Oh Father Enlil, let not thy daughter be *put to death* in the Nether World,
183. Let not thy good metal be *ground up* into the dust of the Nether World,
184. Let not thy good lapis lazuli be *broken up* into the stone of the stone-worker,
185. Let not thy boxwood be *cut up* into the wood of the wood-worker,
186. Let not the maid Inanna be *put to death* in the Nether World."
187. Father Enlil answers Ninshubur:
188. "My daughter, in the "[Great] Above" in the "Great Below"
189. Inanna, in the "[Great] Above" in the "Great Below"
190. The decrees of the Nether World, the decrees, to their place
191. Who, pray, *to* their place?"
192. Father Enlil [did not stand by him] in this matter, he [went] to Ur.
193. *In* Ur, upon his entering the house of the of the land,
194. The Ekishshirgal, the house of Nanna,
195. Before Nanna he weeps:
196. "Oh Father Nanna, let not thy daughter be *put to death* in the Nether World,
197. Let not thy good metal be *ground up* into the dust of the Nether World,
198. Let not thy good lapis lazuli be *broken up* into the stone of the stone-worker,

199. Let not thy boxwood be *cut up* into the wood of the wood-worker,
 200. Let not the maid Inanna be *put to death* in the Nether World."
201. Father Nanna answers Ninshubur:
 202. "My daughter, in the "[Great] Above" in the "Great Below"
 203. Inanna, in the "[Great] Above" in the "Great Below"
 204. The decrees of the Nether World, the decrees, to their place
 205. Who, pray, *to* their place?"
206. Father Nanna [did not stand by him] in this matter, [he went to Eridu].
 207. *In* Eridu, upon his entering the house of Enki,
 208. Before Enki he weeps:
 209. "Oh Father Enki, let not thy daughter be *put to death* in the Nether World,
 210. Let not thy good metal be *ground up* into the dust of the Nether World,
 211. Let not thy good lapis lazuli be *broken up* into the stone of the stone-worker,
 212. Let not thy boxwood be *cut up* into the wood of the wood-worker,
 213. Let not the maid Inanna be *put to death* in the Nether World."
214. Father Enki answers Ninshubur:
 215. "What now has my daughter done! I am troubled,
 216. What now has Inanna done! I am troubled,
 217. What now has the Queen of all the Lands done! I am troubled,
 218. What now has the Hierodule of Heaven done! I am troubled."
 219. *he brought forth dirt* (and) fashioned the *kurgarrû*,
 220. *he brought forth dirt* (and) fashioned the *kalaturru*.
 221. To the *kurgarrû* he gave the food of life,
 222. To the *kalaturru* he gave the water of life.
 223. [Father] Enki sa[ys] to the *kalaturru* and *kurgarrû*:
 224. "..... lay
 225.
 226.
 227.
 228.
 229.
 230.
 231.
 232.
 233.
 234.
 235.
 236.
 237.
 238.
 239.
 240.
 241. To *purify* do not
 242. To *purify* do not
 243. *Upon the corpse hung from a stake direct the fearfulness of the melammu*,
 244. *Sixty times* the food of life, *sixty times* the water of life, sprinkle upon it,
 245. Surely Inanna will arise."
 Break of 20(?) lines.
 246. *from a stake*
 247. The pure Ereshkigal answers the *ka[laturru]* and the *kurgarrû*:
 248. "The corpse"

269. Upon the smitten flesh they
270. *Upon the corpse hung from a stake the fearfulness of the melammu*
271. *Sixty times*, the food of life, *sixty times* the water of life, they sprinkled upon it,
272. Inanna arose.

273. Inanna ascends from the Nether World,
274. The Anunnaki fled,
275. *(And) whoever of the Nether World that had descended peacefully to the Nether World.*
276. When Inanna ascends from the Nether World,
277. Verily the dead *hasten ahead of her*.
278. Inanna ascends from the Nether World,
279. The small *demons* like reeds,
280. The large *demons* like *tablet styluses*,
281. Walked at her side.
282. Who *walked* in front of her, *being without*, held a staff in the hand,
283. Who *walked* at her side, *being without*, carried a weapon on the loin,
284. They who *preceded* her,
285. They who preceded Inanna,
286. (Were beings who) know not food, who know not water,
287. Who eat not sprinkled flour,
288. Who drink not libated [*wine*],
289. Who take away the wife from the loins of the man,
290. Who take way the child from the *breast* of the nursing mother.

291. Inanna ascends from the Nether World.
292. Upon Inanna's ascending from the Nether World,
293. [Her messenger], Ninshubur, threw herself at her feet,
294. Sat in the dust, dressed in *dirt*.
295. The *demons* say to the pure Inanna:
296. "Oh Inanna, *wait before thy city, we would bring him to thee.*"
297. The pure Inanna answers the *demons*:
298. "(He is) my messenger of favorable words,
299. My carrier of supporting words,
300. He *fails* not my directions,
301. He *delays* not my commanded word,
302. He *fills* the Heaven *with complaints for me*.
303. In the assembly shrine he *cried out* for me,
304. In the house of the gods he rushed about for me,
305. He *lowered* his eye for me, he *lowered* his mouth for me,
306. *With* he *lowered* his great for me
307. Like a pauper in a single garment he dressed for me,
308. To the Ekur, the house of Enlil,
309. In Ur, to the house of Nanna,
310. *In* Eridu, to the house of Enki (he directed his step).
311. He brought me to life."

312. "Let us *precede* her, in Umma to the Sigkurshagga let us *precede* her."
313. In Umma, from the Sigkurshagga,
314. Shara threw herself at her feet,
315. Sat in the dust, dressed in *dirt*.
316. The *demons* say to the pure Inanna:
317. "Oh Inanna, *wait before thy city, we would bring him to thee.*"
318. The pure Inanna answers the *demons*:
319. "

320.
 321.
 322. "Let us *precede* her, in Badtibira to the Emushkalamma let us *precede* her."
 323. In Badtibira from the Emushkalamma,
 324. threw *themselves* at her feet,
 325. Sat in the dust, dressed in *dirt*.
 326. The *demons* say to the pure Inanna:
 327. "On Inanna, *wait before* thy city, *we would bring them to thee*."
 328. The pure Inanna answers the *demons*:
 329. to my right and left
 330.
 331. *I would give*, Kullab
 332. Kullab
 333.
 Break of 40(?) lines.
 374.
 375. all the lands
 376. *their dwelling place*
 377. they *carried off*,
 378. they *smite* (?)
 379. a lament they utter
 380. they *hurled*
 381.
 382. *she points her finger*
 383. all the lands, she lifts her eye
 384.

Notes on the Translation ⁷

Lines 1-3.—The a n - g a l, "Great Above", of the Sumerians is the space above the sky and includes the dwelling places of the "sky" gods. The k i - g a l, "Great Below", is the space below the surface of the earth and includes the dwelling places of the chthonic deities. The n a - o f n a - a n - g u b, as Falkenstein has pointed out, is a thematic prefix (my suggestion in RA XXXIV p. 116 is erroneous); it is probably the same prefix which is involved in the Gudea verbal forms listed in GSG §205. The use of the word A N (= d i n g i r (?)) as an epithet of Inanna in the second line of our triplet is unusual, one might rather have expected a term such as n i n - m u o r n u - g i g - a n - n a.

Line 8.—The reading m ū š of the sign M Ū Š in é - M Ū Š - k a l a m - m a is not certain but quite probable.

Line 13.—The reading u l of the sign U L in é - U L - m a š^{ki} is not certain but quite probable.

Lines 14-16.—The translation "decrees" for

the Sumerian m e is preferable to "rites". While the nature of the "decrees" mentioned in lines 14-16 is as yet quite uncertain, we now know at least how Inanna came into their possession, cf. p. 322 No. 12. Since these "decrees" were transported by Inanna on a boat from Eridu to Erech, it is not unlikely that they were conceived as written down on tablets. Perhaps, therefore, it is these tablets which Inanna "fastened at her side", "placed at her hand", etc.⁸ With line 14, cf. VS X No. 199 ii 16 m e - g a l - g a l - l a z a g m u - n i - i n - k e š d, "He (i.e. Anu) fastened the great decrees at his side". In line 15, the - š Ē of š u - n i - š Ē may of course be transliterated as - é š (cf. also lines 94, 163, 191, 192, 204, 205, 273, 314, 324) just as it may be transliterated - u š₄ in u r u - z u - š Ē (lines 296, 317, 327) and - a š₁₀ in s i g₄ - k u r - š à - g a - š Ē (line 312). In line 16, the translation "all" for the D U of m e - D U is predicated on the bare possibility

⁸ Note, however, that in VS X No. 199 iii 19, Inanna boasts: t ū g - m e - k u g k u š - m à m u - n i - i n - l á, "The pure garment of decrees, he (i.e. Enlil) tied about my body." This statement, if it is intended, to be taken literally, would seem to indicate that the "decrees", or at least some of them, were part of a special garment.

⁷ These notes are intended to supplement and, wherever necessary, to modify the commentary on the translation in RA XXXIV, RA XXXVI, and BASOR No. 79.

that it may be a variant of *dù* and on the fact that *D* has the variant *D Û G* which may be read *šár*, "all".⁹

Line 19.—The *gi-diš-ninda-šÈ-gán* seems to be the Akkadian *ginindanakku* despite the fact that the syllabaries do not attest the Sumerian form quite as it appears in our text; cf. Ungnad in ZA XXXI p. 25.

Line 23.—For *tu-di-tum*, cf. the variant *tu-di-da* in VS II No. 32 i 7.

Lines 26-28.—The root of the word represented by *D U*, "to go", in *i-im-D U*, is transliterated as *du* rather than *gin*, since to judge from *ba-du-un*, "thou hast come" (line 82) and *-du-ù-bi*, literally "its goer" (line 83), it ends in the vowel *u*. In the Emesal passages, on the other hand, it does seem to have ended with the consonant *n*, cf. the imperative *D U-na* (lines 48, 57, 70) and the infinitive *D U-na* (line 33). For the unexpected Emesal writings *ga-ša-an* (lines 27-28), cf. AS XII p. 10, heading 9. For *e-me-K U* writings in Emesal passages, cf. *ibid.* p. 7 ff.

Lines 29-31.—The translation "supporting" for *-gi-en-gi-en-na-* (line 31) seems preferable to "true", since the meaning might be expected to parallel the *-šagš-šagš-ga* of the preceding line. Note that *-šagš-šagš-ga* and *-gi-en-gi-en-na-* probably represent the reduplicated *šagš* and *gin* rather than *šagš-a* and *gin-a* (as suggested in RA XXXVI p. 120), the final *a* is probably the genitive *-a(k)*. For the reading and meaning of the variant lines in E, cf. BASOR No. 79 p. 25, note 25; for the restoration *hè-im-ma-ag*, cf. SRT No. 6 line 28.¹⁰

Lines 34-42.—For lines 34-37, cf. BASOR No. 79 p. 26. For the translation "lower" for *HUR* (lines 37-38), cf. perhaps *HUR = qadādu* and the phrase *guddud appušu* in *Ishtar's Descent*. In line 40, the first sign in the verbal form is to be read *gub* (not *túm*). In line 42, note the corrected reading *i-bí-for igi-kug-*.

Lines 42-47.—Note the corrections in the transliteration and translation of this passage as compared with those of RA XXXIV. For the equation *gúr = mátu*, cf. especially SBH No. 4

lines 26-27;¹¹ for the reading *gúr* rather than *gam*, cf. *ba-an-kur* in K 6930. Still difficult is *mu-lu* of line 43; if the construction involved is that of the passive (cf. BASOR No. 79 p. 21, note 5), there seems to be no reason for its use in this particular line and not in any of the following four lines. In line 46, B clearly reads: *giš-nagar-ra-ka* while A inserts *-na-m-* before *-nagar-*; the former reading was chosen since *nagar* seems to parallel the *zadim* of the preceding line, cf. RA XXXVI p. 77, note 11. To judge from the context both the *zadim* and the *nagar* of our myth are denizens of the Nether World.

Lines 48-50.—For *D U-na* (line 48), cf. comment to lines 26-28. In line 49, between *é-* and *-kalam-* is the sign *MUD* (or perhaps the signs *M U Š E N* and *D Û G*), not the signs *NAM* and *D Û G*. In line 50, there is no *é-* preceding *na nna-šè*.

Lines 52-56.—Cf. comment to lines 43-47.

Line 57.—For *D U-na*, cf. comment to lines 26-28.

Lines 60-64.—Cf. comment to lines 43-47.

Lines 65-67.—Note the corrected translation of these lines as compared with that of RA XXXIV. It assumes the *-da-* of *-da-ma-al-* has been omitted by scribal error; that *e-ne* (line 57) refers to Enki; that *ma-ra* (for the expected *mà-e*) is a dative of reference (cf. comment to lines 284-285) and that *hu-mu-un-ti-li* is a present-future asseverative form of the third person singular.¹²

Lines 68-71.—For *i-im-du* (line 68) and *D U-na* (line 70), cf. comment to lines 26-28. Note the corrected word division in line 71; the meaning might be expected to approximate: "Do not delay my commanded word." As the line stands at present, however, it is difficult to analyze.

Lines 72-74.—As the translation indicates the *u* of *um-ma-te* is the conditional *u*, cf. GSG §426; the suggestion offered in RA XXXVI p. 124 seems less likely. Note the corrected reading *ba-an-uš* for *ba-an-gál* in line 73.

Line 80.—The *-aš (= -šè)* of *ki-dutu-*

⁹ The Sumerian reads *umun-e-e-ne-ēm-ma-ni* *één-par(l)* *TUL-ba-ām-mi-ib-gúr-gúr*. The word *één-par* is the phonetic form of *ambar* (Akkadian loan word *apparu*). Note, therefore, that the equations to be derived from this passage are: *één-par = apparu* and *TUL-ba = ina šuklišu*, and that ŠL 85: 144 and 74: 348 are to be eliminated.

¹² The final *-en* in A's variant, if not a scribal error, remains difficult.

⁹ Cf. also VS X No. 199 ii 17: *me-šár-ra-gir-ni nam-mi-in-gar*, "He (i.e. Anu) placed all the decrees at his feet."

¹⁰ In HGT No. 1 (the "deluge" tablet), line 5 of col. iii is probably to be restored: *na-ri-ga-mu geštug X hè-im-ma-ag*, rather than as suggested in BASOR No. 79 p. 26.

è-a-aš is not the postposition as assumed in RA XXXVI, but the verb šè, "to do", "to make", etc. A more literal translation of ki-⁴utu-è-a-aš is, therefore, "the place where the sun makes (his) rising"; for this idiomatic and from our point of view pleonastic use of the verbs šè and a g, cf. Poebel in AOF IX p. 266.

Line 88.—Note the corrected reading of the line; the translation of the first half of the line in RA XXXIV is therefore erroneous.

Line 91.—Instead of nin-m à the form might have been expected to read nin-mu-ra.

Lines 126-160.—According to this passage, Inanna wore seven bits of apparel which were removed piece by piece as she passed through each of the seven gates of the Nether World. On the other hand, the passage describing Inanna's dress preparatory to her descent consists of nine lines, each of which seems to describe a specific unit of apparel. In A, the removal of the hi-li-sag-ki-na and the šim(?) -e-ḥé-im-DU-ḥé-im-DU is omitted. In G, it is to be noted, the gi-diš-ninda-ŠÈ-gán was removed even before she entered the first gate, although according to A it was removed at the second gate, and according to I it was removed at the seventh gate. According to G, therefore, it is not impossible that eight bits of apparel were removed. For the expressions lú ba-da-an-ši-ir and ta-àm-me-a, cf. BASOR No. 79 p. 21. The translation "do not question" for ka-zu na-an-...-e-en is a guess based on the context; the grammatical relationship between ka-zu and the partly broken verbal form still remains uncertain.

Line 161.—Cf. RA XXXVI p. 79, comment to col. iii 19, and especially note 6; cf. also BASOR No. 79 p. 24.

Lines 162-168.—Cf. BASOR No. 79 p. 24 ff. In line 163 it is perhaps the plural form of the verb which is to be restored; note, however, the singular mu-ši-in-bar in line 164. For the unjustified Emesal i-bí (line 164), cf. comment to lines 26-28.

Lines 169-178.—Note the incorrect Emesal writings i-bí (line 176) and mu-lu (line 178). In line 177, on the other hand, note the correct writing lú; the corresponding line 38, which is part of Inanna's speech, uses the Emesal mu-lu.

Lines 188-191.—The translation of this significant passage will be impossible as long as the

meaning of the compound al—dug₄ remains uncertain.

Lines 209-245.—Cf. RA XXXVI p. 68 ff. In line 233, note that the restoration -ne- is preferable to -na- in mu-ne-dé-e, although to judge from lines 277, 318, and 328, it is not impossible that the scribe wrote the grammatically incorrect -na-. For line 243, cf. BASOR No. 79 p. 24, line 20.

Lines 246-323.—In line 247, the restoration of -ne- in mu-ne-ni-i-b-gi₄-gi₄ is preferable to -na-, cf., however, preceding note. Line 268 probably contains Ereshkigal's speech, note the Emesal á m for the eme-KU ní g. Lines 269-271 describe the action of the *kalaturru* and *kurgarrú*; cf. especially line 270 with line 243 and line 271 with line 244. In line 280, the last sign is KE₄, not GIM. In line 284, -ene-ra seems to be a dative of reference; so also -⁴inanna-ra of line 285; cf. comment to lines 65-67. In line 290, the sign preceding -lá- is DA, not GA. In line 295, the translation assumes that galla-e-ne is a plural and that it is the subject of gù mu-un-na-dé-e, although the latter is in the singular. For ga-ba-ab-túm-mu-dé (line 296) cf. RA XXXIV p. 112. In line 297, galla-e-ne is assumed to be a plural in spite of the singular infix -na- (for the expected -ne-). For lines 298-307, cf. lines 29-39 and lines 170-178. Line 308 is a contraction for the entire passage contained in lines 179-192; line 309 is a contraction for that contained in lines 193-206; line 310 is a contraction for that contained in lines 207-213. In line 311, the translation assumes that ma-ra is a dative of reference and that the final -en of the verbal form is a second person singular accusative element; cf. comment to line 67. For ga-an-ši-súg-dè-en (line 312), cf. RA XXXIV p. 133 and especially note 2. In line 312, note that the corrected reading of Shara's temple in Umma is sig₄-kur-šà-ga; cf. TRS No. 15 obv. ii 12: é-bi umma sig₄-kur-šà-ga¹³ and the Emesal form SIG₄(!)-kur-šà(!)-ba in PBS X 2 No. 4 rev. 16. In line 324, if no error is involved the verb is a third person plural preterit.

Lines 374-384.—In its present fragmentary state it would be futile to attempt any definitive interpretation of the passage.

¹³ A collation of the duplicate STVC No. 66 rev. i 15 shows it to begin with: é-bi umma (!)^{ki}-a sig₄(!)-kur-šà-ga-ke.

EXCURSUS A

The Decipherment of Sumerian

The decipherment of Sumerian differed from that of Assyrian and Egyptian in one significant detail, a detail which proved to be one of the factors in hampering the progress of Sumerology to no inconsiderable extent. For in the case of both Egypt and Assyria, the investigating scholars of western Europe had at their disposal much relevant material from Biblical, classical and post-classical sources. Not only were such names as Egypt, Ashur, Babylon, etc. well known, but at least to a certain extent and with much limitation and qualification, even the history and culture of the peoples were not altogether unfamiliar to them. In the case of the Sumerians, however, the situation was quite different; *there was no recognizable trace of Sumer or its people and language in the entire Biblical, classical, and post-classical literature.* The very name Sumer was erased from the mind and memory of man for over two thousand years. The discovery of the Sumerians and their language came quite unexpectedly and was quite unlooked for, and this more or less irrelevant detail was at least partially responsible for the troubled progress of Sumerology from the earliest days to the present moment.

Historically, the decipherment of Sumerian resulted from that of Assyrian which in turn followed the decipherment of cuneiform Persian. Briefly sketched, the process was as follows: In 1765, the Danish traveller and scholar, Carsten Niebuhr, succeeded in making careful copies of several inscriptions on the monuments of Persepolis. These were published between the years 1774 and 1778, and were soon recognized as trilingual, *i.e.* the same inscription seemed to be repeated in three different languages. It was not unreasonable to assume, since the monuments were located in Persepolis, that they were inscribed by one or more kings of the Achaemenid dynasty and that the first version in each inscription was in the Persian language. Fortunately, at approximately the same time, Old Persian was becoming known to western European scholars through the efforts of Duperron who had studied in India under the Parsees and was preparing translations of the Avesta. And so by 1802, with the help of the newly acquired knowledge of Old Persian and by a keen manipulation of the Achaemenid proper names as handed down in Biblical and classical literature,

the German scholar, Grotefend, succeeded in deciphering a large part of the Persian version of the inscriptions. Additions and corrections were made by numerous scholars in the ensuing years. But the crowning achievement belongs to H. C. Rawlinson. A member of the English Intelligence Service, Rawlinson was first stationed in India where he mastered the Persian language. In 1835 he was transferred to Persia where he learned of the huge trilingual inscription on the Rock of Behistun and determined to copy it. The Persian version of the Behistun inscription consists of 414 lines; the second, now known as the Elamite version, consists of 263 lines, while the third, or Assyrian version, consists of 112 lines. During the years 1835-7, at the risk of life and limb, Rawlinson succeeded in copying 200 lines of the Persian version. He returned in 1844 and completed the copying of the Persian as well as the Elamite version. The Assyrian inscription, however, was so situated that it was impossible for him to copy it and it was not until 1847 that he succeeded in making squeezes of the text. To return to the decipherment of cuneiform Persian, by 1846 Rawlinson published his memoir in the *Journal of the Royal Asiatic Society* which gave the transliteration and translation of the Persian version of the Behistun inscription together with a copy of the cuneiform original.

Long before the final decipherment of the Persian text, however, great interest had been aroused in western Europe by the third version of the Persepolis inscriptions. For it was soon recognized that this was the script and language found in numerous inscriptions on bricks, clay tablets, and clay cylinders which were finding their way into Europe from sites that might well be identified with Nineveh and Babylon. In 1842, the French under Botta began the excavation of Khorsabad and in 1845, Layard began his excavations of Nimrud and Nineveh. Inscribed monuments were being found in large quantities in all three sites; moreover Layard was uncovering at Nineveh a large number of inscribed clay tablets. By 1850, therefore, Europe had scores of inscriptions coming largely from Assyrian sites inscribed in the very same script and language as the third version of the Persepolis and Behistun inscriptions. The decipherment of Assyrian, the name soon given to this language, was simplified on the one hand by the fact that it was recognized quite early in the process that it belonged to the Semitic group of languages.

On the other hand, it was complicated seriously by the fact that the orthography, as was soon recognized, was syllabic and ideographic rather than alphabetic. The leading figure in the decipherment of Assyrian was the Irish scholar, Edward Hincks. But once again a major contribution was made by Rawlinson. In 1851 he published the text, transliteration and translation of the Assyrian version of the Behistun inscription, the large trilingual to which he alone had access.

As for the second, or Elamite, version of the Behistun inscription, it offered relatively little difficulty as soon as progress was made in the decipherment of Assyrian, since it uses a syllabary based on the latter system of writing. The major figures in its decipherment were Westergaard and Norris. As early as 1855, Norris, the secretary of the Royal Asiatic Society, published the complete text of the second version of the Behistun inscription which had been copied by Rawlinson together with a transliteration and translation; this remained practically the standard work on the subject until Weissbach published his *Achamenideninschriften zweiter Art* in 1896.

As will be noted, nothing has as yet been heard or said of the Sumerians. As early as 1850, however, Hincks began to doubt that the Semitic Assyrians had invented the cuneiform system of writing. In the Semitic languages the stable element is the consonant while the vowel is extremely variable. It seemed unnatural, therefore, that the Semites should invent a syllabic system of orthography in which the vowel seemed to be as unchanging as the consonant. Moreover, if the Semites had invented the script, one might have expected to be able to trace the syllabic values of the signs to Semitic words. But this was hardly ever the case, the syllabic values all seemed to go back to words or elements for which no Semitic equivalents could be found. Hincks thus began to suspect that the cuneiform system of writing was invented by a non-Semitic people who had preceded the Assyrians in Mesopotamia. In 1855, Rawlinson published a memoir in the *Journal of the Royal Asiatic Society* in which he speaks of his discovery of non-Semitic inscriptions on the bricks and tablets from sites in southern Babylonia such as Nippur, Senkereh, and Erech. In 1856, Hincks took up the problem of this new language, recognized that it was agglutinative in character and gave the first examples from bilinguals which had come

to the British Museum from the Nineveh Excavations. The name of the language was variously designated as Scythic or Accadian. But in 1869, the French scholar Oppert, basing himself on the royal title "king of Sumer and Accad" and realizing that Accad was equated with the Semitic Assyria, rightly attributed the name Sumerian to the language spoken by the non-Semitic people who had invented the cuneiform script. Nevertheless, Oppert was not immediately followed by most of the Assyriologists, and the name Accadian which is now used to designate the Semitic population and language of Assyria and Babylonia, continued to be used for Sumerian for many years to come.¹⁴

For several decades following the discovery of the existence of Sumerian, practically all the source material for its decipherment and study consisted of the bilinguals and syllabaries from the so-called Ashurbanipal library which was discovered and excavated in Nineveh. This material dates from the seventh century B.C., more than fifteen hundred years after the disappearance of Sumer as a political entity. As for the material from the Sumerian sites, it consisted almost entirely of a very small group of bricks, tablets and cylinders from the Sumerian and post-Sumerian periods which had found their way into the British Museum. In 1877, however, began the excavation of Tello, ancient Lagash, an excavation which has been conducted by the French intermittently and with long periods of rest almost to the present day. It was at this site that the first important Sumerian monuments were excavated, the monuments and inscriptions of the *ishakku's* or "princes" of Lagash. Here more than one hundred thousand tablets and fragments were dug up dating from the pre-Sargonid, Sargonid and Ur III periods.¹⁵

¹⁴ As a matter of historic curiosity it is noteworthy to mention that in spite of all evidence to the contrary, the well known Orientalist, J. Halévy continued to deny the existence of a Sumerian people and language in Babylonia, as late as the first decade of the twentieth century. According to his biased and subjectively motivated views, no people other than the Semites had ever been in possession of Babylonia. As for the so-called Sumerian language, it was merely an artificial invention of the Semites devised for esoteric purposes.

¹⁵ The first forty thousand tablets were discovered by the Arab workers while De Sarzec, the excavator happened to be away from the mound. They succeeded in getting them all into the hands of dealers, and as a result there is not an important collection in Europe or America which does not have some Lagash tablets. In the Museum of the Ancient Orient, the tablets excavated at Lagash are

The second major excavation of a Sumerian site was that conducted by the University of Pennsylvania at Nippur between the years 1889 and 1900. From the point of view of inscriptional finds, this excavation is probably the most important conducted on any Sumerian site to date. Approximately thirty thousand tablets and fragments were excavated at Nippur. Because of the variety of their contents they furnish more significant source material than the much larger number of tablets excavated at Lagash. Of the thirty thousand Nippur tablets, some are Semitic and date from the Hammurabi, Kassite, and Neo-Babylonian periods. Most of the Nippur tablets, however, are Sumerian. They contain a great variety of economic documents dating from the pre-Sargonid, Sargonid and Ur III periods, i.e. from approximately 2800 to 2000 B.C. They contain, too, a considerable number of lexical and grammatical texts; it was this group of Nippur tablets which furthered to no small extent the formulation of the principles of Sumerian grammar. *But the unique and most significant part of the Nippur material consists of more than two thousand "literary" tablets and fragments dating from the early post-Sumerian period, i.e. from about 2000 B.C.*¹⁶

Following Nippur, the excavations by the Germans of Fara (ancient Shuruppak) in 1902-3 and that by the University of Chicago at Bismaya (ancient Adab) in 1903-4, uncovered important Sumerian economic and lexical material dating largely from the pre-Sargonid and Sargonid periods. Excavations at Kish, begun by the French in 1911 and continued under Anglo-American auspices from 1922 to 1930, have yielded important inscriptional material. In

Jemdet Nasr, not far from Kish, a large group of semi-pictographic tablets that go back to the early beginnings of Sumerian writing, have been excavated. Ur, the famous site excavated by a joint expedition of the British Museum and the University Museum between the years 1919 and 1933, yielded many historical and economic inscriptions and some literary material. In Asmar and Hafaji, east of the Tigris, a large number of economic tablets dating largely from the Sargonid and Ur III periods, were excavated by the Oriental Institute of the University of Chicago in recent years. Finally in Erech, where the Germans conducted excavations from 1928 until the outbreak of the war, a large group of pictographic Sumerian tablets antedating those found at Jemdet Nasr have been uncovered.

This brief survey furnishes a bird's-eye view of the Sumerian inscriptional finds uncovered and brought to light by legitimate excavations. In addition, scores of thousands of tablets have been dug up clandestinely by the native Arabs in the mounds of Sumer, especially in the ancient sites of Larsa, Sippar, and Umma. It is therefore difficult to estimate the number of Sumerian tablets and fragments now found in museums and in private collections; a quarter of a million is probably a conservative guess. What, now, is the nature of the contents of this vast amount of Sumerian inscriptional material? What significant information can it be expected to reveal?

In the first place it is important to note that *more than ninety-five percent of all the Sumerian tablets are economic in character, i.e. they consist of notes and receipts, contracts of sale and exchange, agreements of adoption and partnership, wills and testaments, lists of workers and wages, letters, etc.* Because these documents follow a more or less expected and traditional pattern, which is found also in the Semitic documents of the same character, their translation, except in the more complicated cases, is not too difficult. It is the contents of these tablets which give us a relatively full and accurate picture of the social and economic structure of Sumerian life in the third millennium B.C. Moreover the large quantity of onomastic material to be found in these economic documents furnishes a fruitful source for the study of the ethnic distribution in and about Sumer during this period.

Of the Sumerian inscriptions that are not economic in character, one group consists of approximately six hundred building and dedicatory inscriptions on steles, bricks, cones, vases, etc.

stacked high in drawer after drawer; it is difficult to estimate their number, but it may be close to one hundred thousand.

¹⁶ It is a curious fact that of all the expeditions excavating in Sumer in the course of the past century, the only one which uncovered Sumerian literary material in large quantity was that conducted by the University of Pennsylvania at Nippur. Relatively little has been excavated in the other sites of Sumer. No doubt this unfortunate fact is merely a matter of archaeological accident, the excavators evidently failed to come upon the temple and palace libraries. *From the point of view of the spiritual and religious history of the Sumerians as well as from that of Sumerian literature, the site that holds most promise to the future excavator is Eridu. As the seat of the cult of Enki, the Sumerian "Lord of Wisdom", the keeper of the divine decrees which helped to found and govern Sumerian civilization, it should prove to be a veritable storehouse of literary and religious tablets.*

It is from this relatively small group of inscriptions that the political history of Sumer has been largely recovered. The translation of these inscriptions, too, offers no great difficulties, since the contents are usually brief and simple. Moreover, the structure and pattern of the Sumerian dedicatory inscriptions are followed to a large extent by the later Semitic building inscriptions; the bilingual material, too, is of considerable help. All in all, therefore, except in the more complicated cases, the Sumerian historical material is relatively simple to translate and interpret.

The most significant material for the study of Sumerian culture, however, especially in its more spiritual aspect, consists of a group of approximately three thousand "literary" tablets and fragments dated about 2000 B.C. which are inscribed with Sumerian epics and myths, hymns and lamentations, proverbs and words of wisdom. Of these three thousand pieces, approximately nine hundred are distributed as follows: Some three hundred very tiny fragments have been found in Kish and were published by De Genouillac in 1924. Approximately two hundred pieces were bought by the Berlin Museum from dealers; these were published by Zimmern in 1912 and 1913. Approximately one hundred were bought by the Louvre from dealers; these were published by De Genouillac in 1930. Less than a hundred pieces have found their way to the British Museum and the Ashmolean Museum and have been published by King, Langdon, and Gadd. To these must be added an uncertain number (two hundred (?)) of tablets and fragments excavated recently in Ur which will be published by Gadd of the British Museum in the near future.

The remaining two thousand and one hundred tablets and fragments, by far the major part of our source material, was excavated by the University of Pennsylvania at Nippur almost fifty years ago. Of this number, over one hundred have found their way to the University of Jena in Germany, approximately eight hundred are located in the Museum of the Ancient Orient at Istanbul, and almost eleven hundred are located in the University Museum at Philadelphia. Of this Sumerian literary material lying in the University Museum, approximately four hundred pieces have been copied and published by a number of scholars in the course of the past four decades. It is the remaining six hundred and seventy-five pieces in the University Museum, which, with the aid of a grant from the American Philo-

sophical Society, I have sought out and begun to copy. It will take some years to complete the copying of this large quantity of source material; its achievement will enable us to reconstruct and translate a large and significant group of Sumerian literary compositions. It is well worth noting that these Sumerian literary creations are significant not only for their remarkable form and illuminating contents. They are quite unique, too, in that they have come down to us as actually written by the scribes of four thousand years ago, unmodified and uncodified by later redactors with axes to grind and ideologies to satisfy. *Our Sumerian literary compositions thus represent the oldest literature of any appreciable and significant amount ever uncovered.*

EXCURSUS B

Sumerian Epics and Myths

Undoubtedly one of the major significant and enduring humanistic achievements of the past hundred years consists of the discovery and decipherment of the Babylonian literary compositions inscribed on tablets that have lain buried in the ruins of Assyria and Babylonia for more than twenty-five hundred years. Inscribed in the Semitic Accadian language and in the cuneiform script, both of which had been unknown and forgotten for a period of two thousand years, the decipherment and translation of these compositions was so rapid that their contents are now available to the layman as well as the scholar. The *Creation Epic*, the *Gilgamesh Epic*, the myth of *Ishtar's Descent to the Nether World*, to name but three of the better known compositions, are now listed and cited, quoted and analyzed in all the major works on mythology and religion. The men responsible for this achievement, Smith and Pinches, Schrader and Delitzsch, King and Thompson, Haupt and Jensen, to name some of the major figures, have gained lasting and well-earned recognition in the humanistic hall of fame.

As the decipherment and translation of the Babylonian literary compositions progressed, however, a strange phenomenon became increasingly apparent. A closer analysis of the poems revealed that while the language was Semitic, while the form and redaction were Semitic, while, too, the tone and temper, the overtones and undertones, were Semitic in character, the contents themselves clearly be-

trayed their Sumerian origin. For in practically all the Babylonian compositions, many of the major protagonists bear Sumerian, not Semitic, names.¹⁷ Thus, of the deities involved in the epics and myths, by far the greater number belong to the Sumerian pantheon. Gilgamesh, the great Babylonian hero, bears a Sumerian name. His father bears the Sumerian name Lugalbanda, his mother is the Sumerian goddess Ninsun. His friend and companion bears the good Sumerian name Enkidu. The facts and proofs lie clear and on the surface, it required no particular profundity, no extraordinary insight, to realize that the Babylonian compositions are of Sumerian origin.

What prevented scholars from effectively drawing this obvious conclusion is the fact that almost nothing was known of any Sumerian literary compositions. By the beginning of our century, the political history of the Sumerians had gradually been recovered, largely through the efforts of the very eminent French Assyriologist, Thureau-Dangin. The economic and administrative documents of the Sumerians, excavated by the hundreds of thousands, were being published and zealously studied. But the literary creations of the Sumerians continued to remain practically unknown. And yet there was no dearth of source material. Almost three thousand Sumerian literary tablets and fragments dating from the early post-Sumerian¹⁷ period, *i.e.* from approximately 2000 B.C. and antedating the Babylonian Semitic compositions by more than a millennium, were lying in the store rooms of the European and American museums. In Nippur alone, the University of Pennsylvania had excavated over two thousand tablets and fragments which were divided between the Museum of the Ancient Orient at Istanbul and the University Museum at Philadelphia. The British Museum, the Louvre, and the Berlin Museum had obtained between them

more than seven hundred Sumerian literary tablets and fragments, largely from the hands of dealers. To repeat, therefore, there was no dearth of source material.

What then hampered and impeded the decipherment of the Sumerian literary compositions? Why has so little progress been made in the reconstruction and translation of their contents? Primarily this unfortunate situation is due to the fact that only a small fraction of this source material has been copied and published to date. Tablets, and especially those inscribed with the Sumerian literary compositions, which are largely unbaked, rarely come out whole from the ground. Usually they are in a fragmentary, and not infrequently in a very fragmentary, state. Offsetting this disadvantage is the fact that the ancient scribes made more than one copy of any given composition. The breaks in one tablet may therefore frequently be restored from duplicating pieces which may themselves be in a very fragmentary condition. In the case of *Inanna's Descent to the Nether World*, for example, I utilized fourteen different fragments. In the case of the *Lamentation Over the Destruction of Ur* which I recently published, the text was reconstructed from twenty-two different fragments. In reconstructing one of the Ninurta epics (*cf.* No. 7 on p. 321) I utilized *forty-five* different fragments. To take full advantage of these duplications and the consequent restorations, however, it is essential to have as much as possible of the source material available. But of the Nippur literary tablets and fragments excavated by the University of Pennsylvania, over two thousand in number, only about five hundred have been copied and published to date. And while all of the approximately seven hundred pieces in the British Museum, Louvre, and Berlin Museum, have now been published, some of the more important texts did not appear until a relatively recent date. Under these circumstances, the reconstruction and translation of the Sumerian literary compositions on any major scale, were obviously impossible.

But even in case of the material long copied and published, the attempted translations were rarely scientific and trustworthy. In the first place, the translator was hampered by grammatical difficulties. For Arno Poebel's *Grundzüge der Sumerischen Grammatik*, the work that is now generally conceded to be the first and as yet only trustworthy attempt to place Sumerian grammar on a scientific basis, did not appear

¹⁷ Very little literary material belonging to the Sumerian period proper, *i.e.* to the third millennium B.C., has been unearthed to date. No doubt this is a matter of archaeological accident, it is still lying underground in the excavated and unexcavated mounds of Sumer. The mound of Eridu especially may be expected to yield to the future excavator large quantities of this invaluable literary material dating from the Sumerian period. The major part of our present source material for the reconstruction of the Sumerian literary compositions, however, was written, though not necessarily composed, by the Semitic scribes of the early post-Sumerian period for whom Sumerian was the classical literary and religious language.

before 1923. Until then the translation of the Sumerian unilingual material was, grammatically speaking, largely a matter of guess work. The *Grundsätze*, however, is conceived and written from a logical rather than a pedagogical approach. Moreover, the principles laid down in it presuppose a thorough understanding of the Sumerian system of writing, a subject upon which the book barely touches. Consequently it presented so many difficulties to its readers that not a few failed to realize its significance and value, the more so since it proved to be no simple matter to apply the grammatical laws to the actual texts. In the course of the past decade this situation has been eased to no small extent by Poebel's more explicit studies and, if I may be permitted to say so, by my own efforts at clarification. While obviously enough many a point still remains obscure, the problem of Sumerian grammar can on the whole be rightly described as adequately settled.

In the second place, the translator was met by many lexical difficulties; indeed at the present moment the lexical problem is far more serious than the grammatical. One of the major sources for Sumerian lexicology consists of the bilingual texts where the Sumerian words are translated into Accadian. But a large number of words found in the Sumerian literary texts still have no Accadian equivalents. On the other hand many of them have, or at least seem to have, more than one Accadian equivalent. In these cases, the difficulties involved in the choice of the correct equation are not infrequently disastrous; a wrong choice may color falsely an entire context.¹⁸

In view of these difficulties, textual, grammatical and lexical, it is, therefore, profoundly gratifying to be in a position to announce after almost four years of continuous research in the Museum of the Ancient Orient at Istanbul and in the University Museum at Philadelphia, the reconstruction of the larger part of the contents of twenty-three Sumerian epics and myths. In the Museum of the Ancient Orient I copied one hundred and seventy Sumerian tablets and fragments of which approximately thirty are epics and myths.¹⁹ In

the University Museum, after examining the entire Nippur collection consisting of fifteen thousand tablets, I succeeded in cataloguing approximately one thousand and seventy-five pieces which contain Sumerian literary compositions dating from the early post-Sumerian period. About four hundred of these have been copied and published in the course of the past several decades by Poebel, Radau, Myhrman, Lutz, Barton, Langdon, Legrain, and especially by the late Edward Chiera. The remaining six hundred and seventy-five pieces, it is hoped, will be copied by me in the course of the coming several years. Of these six hundred and seventy-five pieces, approximately one hundred and seventy-five are epics and myths, three hundred are hymns, fifty are lamentations, and the remaining one hundred and fifty are proverbs and "wisdom" texts. In the past year my efforts were concentrated on the epics and myths. By utilizing all the extant published material together with the part of the unpublished material which I copied in the Museum of the Ancient Orient at Istanbul and all the unpublished pieces in the University Museum at Philadelphia,²⁰ the following epics and myths can now be reconstructed in large part:

Epics

1. *Enmerkar*.—Two large portions of an epical composition dealing with the exploits of this Sumerian hero in the course of subjugating the city of Aratta to Erech, can now be reconstructed from twenty-five published and unpublished texts. The larger portion consists of approximately three hundred and fifty, and the smaller portion of one hundred and fifty, consecutive

of course await the end of the war, will help to restore many of the passages now missing. Thus in the course of the very last days of my stay in Istanbul I discovered a large prism, excellently preserved, whose text when copied should restore almost completely the Enmerkar epic (No. 1 on p. 320).

²⁰ It is to be noted that to date only a part of the unpublished one hundred seventy-five tablets and fragments inscribed with Sumerian epics and myths, have been copied by me. Those pieces utilized in the reconstruction of the epics and myths which have not been copied, have been very carefully transliterated. The publication of each of the epics and myths, consisting of the hitherto unpublished original cuneiform text together with a transliteration, translation and commentary—the present publication of *Inanna's Descent to the Nether World* furnishes an excellent illustration of the method to be followed—will appear, it is hoped, in the course of the coming several years.

¹⁸ The situation is complicated and worsened by the fact that we still lack a trustworthy Sumerian lexicon. The entire problem of Sumerian lexicology and lexicography is the subject of a forthcoming paper by the writer.

¹⁹ Approximately 500 "literary" tablets and fragments from Nippur still remain uncopied in the Museum of the Ancient Orient. The copying of this material which must

lines; in both cases the lines are about half complete.

2. *Lugalbanda and Enmerkar*.—The contents of this composition, hitherto usually designated *Lugalbanda and the Zu-bird* may be briefly sketched as follows. Lugalbanda, desirous of journeying to Aratta, is anxious to learn the divine instructions. He goes to Mt. Sabu and wilily succeeds in befriending the Zu-bird who knows the decisions of the gods and advises Lugalbanda accordingly. The latter now returns to Erech, whose king Enmerkar is in desperate straits. For fifty years the Martu have been ravaging all Sumer and Accad, and now Erech is in danger of falling. He was therefore seeking desperately some messenger who would journey to Aratta all alone and inform his sister Inanna of his dire plight. Lugalbanda volunteers for the task and succeeds in carrying Enmerkar's message to Inanna of Aratta, and in obtaining from her the appropriate instructions for the solution of Enmerkar's difficulties.

3. *Lugalbanda and Mt. Hurrum*.—Hitherto largely unknown, this tale narrates the adventures of Lugalbanda and his companions who had set out for an expedition to Mt. Hurrum, the same mountain where his son Gilgamesh later kills the monster Huwawa. Close to three hundred lines can now be reconstructed, half of which are complete.

4. *Gilgamesh and Agga of Kish*.—This tale consists of one hundred and fifteen lines, all practically complete. Briefly sketched, the story runs as follows: Agga, the king of Kish, has sent messengers to Gilgamesh demanding that Erech acknowledge the overlordship of Kish. Gilgamesh thereupon gathers a council of the elders of Erech and urges upon them the refusal of Agga's demands. Erech is then besieged by Agga and his warriors, and Gilgamesh is forced to acknowledge Agga as king of Erech.

5. *Gilgamesh and Huwawa*.—The first part of the composition consists of one hundred and seventy-eight lines, all almost perfectly preserved; it is reconstructed from twelve published and unpublished texts. It differs considerably in tone and contents from the traces of the Huwawa episode in the Semitic version of the Gilgamesh epic. The story runs as follows: Gilgamesh had set his heart to journey to the kur-lú-ti-la, perhaps the mountain of immortality. He tells Enkidu of his determination, and the latter advises him to acquaint the sun god Utu of his project, since he is the builder

of the mountain. Thereupon Gilgamesh offers prayers and sacrifices to Utu who helps him cross the seven mountains. At this point Enkidu urges Gilgamesh to abandon his dangerous undertaking, since the mountain is guarded by the fierce monster Huwawa. Gilgamesh refuses to consider Enkidu's advice and continues his journey. He comes upon Huwawa and begins to attack him. But Huwawa breaks into tears and pleads with Gilgamesh for mercy. Gilgamesh is inclined to listen to his plea but Enkidu advises against it. Gilgamesh and Enkidu then bring Huwawa before Enlil and Ninlil. (Here the extant part of the story unfortunately comes to an end.)

6. *Gilgamesh, Enkidu, and the Nether World*.—This composition consists of approximately three hundred lines of which about two hundred are in perfect condition; it is reconstructed from sixteen different fragments. The first half has been published by me under the title *Gilgamesh and the Huluppu-tree*; the latter half duplicates almost verbatim the twelfth tablet of the Semitic version of the *Gilgamesh Epic*.

7. *The Feats and Exploits of Ninurta*.—This epic, usually referred to as lugal-e-u-m-e-lám-bi-nir-gál, consists of approximately six hundred and forty lines of which about four hundred are practically complete; it is reconstructed from forty-five texts of which more than half are still unpublished. It is this composition which was probably utilized in large part by the Semitic scribes in redacting their *Creation Epic*. Roughly the contents may be divided into four parts: 1. Ninurta, with the insistent advice and encouragement of his weapon the Sharur, attacks and destroys Kur, probably the Sumerian equivalent of the Accadian monster Tiamat. 2. He builds the Hursag and appoints the goddess Ninmah as its queen (hence her name Ninhursag). 3. He blesses and curses the stones. 4. He is praised and exalted for his heroic deeds.

8. *The Return of Ninurta to Nippur*.—This is the much shorter composition usually referred to as an-gim-dím-ma; it is reconstructed from twelve fragments. It treats largely of Ninurta's return to Nippur after he had vanquished the monster Kur and of the exaltation of his temple Eshumedu.

9. *Inanna and Entiki*.—Hitherto largely unrecognized, this tale narrates of the struggle of Inanna with Entiki, probably another name for Kur. It consists of one hundred and ninety

lines of which approximately one hundred are in perfect condition and is reconstructed from twelve fragments, largely unpublished.

Myths

1. *The Deluge*.—The tablet published by Poebel in HGT No. 1 still remains the only extant text for this important myth; neither in Istanbul nor in Philadelphia have I succeeded in uncovering any additional material.

2. *Enki and Ninhursag*.—This is the so-called and largely misinterpreted *Sumerian Epic of Paradise*. It consists of two hundred and seventy-six lines and its contents are truly remarkable for their simplicity and uniqueness. They may be briefly sketched as follows: 1. Enki sees to it that holy Dilmun is well supplied with water. 2. He begets Uttu, a female deity largely responsible for the earth's vegetation. 3. He is cursed by the goddess Ninhursag after decreeing the fate of numerous plants. 4. He is healed by Ninhursag who creates numerous deities for that purpose.

3. *Enlil and Ninlil*.—A fascinating myth in explanation of the birth of the moon-god Nanna and of the three chthonic deities, Nergal, Ninazu and one whose name is illegible; its one hundred and fifty-two lines of text are almost complete.

4. *Emesh and Enten*.—Hitherto practically unknown, this agricultural myth consisting of three hundred and eight lines of which approximately half are complete, is reconstructed from five fragments; four of these are still unpublished. Emesh and Enten are two demigods created by Enlil. Enten is appointed as the *engar-zì*, "the trustworthy field worker" of Enlil, but Emesh disputes his title until finally Enlil is forced to intervene in favor of Enten. In the course of Enten's argument with Emesh he interpolates a prayer for the welfare of Ibi-Sin, the last of the kings of Ur.

5. *Lahor and Ashnan*.—Only one hundred and forty-five lines of this myth are as yet available; these are reconstructed from nine published and unpublished texts. The extant portion treats of the creation of the two cultural beings in charge of grain and cattle, and their descent to the earth at the command of Enlil and Enki.

6. *Enki and Ninmah*.—A very important myth dealing with the creation of man. The extant part consists of one hundred and thirty-one lines, most of which are fairly complete.

7. *Enki and Sumer*.—A myth treating largely of the civilizing of Sumer by Enki who appoints numerous cultural deities to their respective duties. Approximately two hundred and sixty-five lines can now be reconstructed of which about half are fairly complete.

8. *Enki and Eridu*.—This myth consisting of one hundred and twenty-eight lines can now be completely restored from twenty-one different fragments. It describes the building of Enki's temple at Eridu and of his trip to Nippur where he is welcomed by Enlil who blesses his handiwork.

9. *The Creation of the Pickax*.—This composition, too, can now be completely reconstructed; it consists of one hundred and eight lines based on twenty different fragments. It treats of the creation of the *al*, "the pickax", by Enlil, and of its dedication by the gods.

10. *The Pickax and the Plow*.—About two hundred and twenty-two lines of this hitherto almost unknown composition can now be reconstructed from ten fragments; about half of the lines are fairly complete. The extant portion describes a colloquy between the two implements, each extolling its particular virtues. (It is not impossible, therefore, that the composition may turn out to be a fable rather than a myth.)

11. *Inanna's Descent to the Nether World*.—Cf. pages 295-312 of this publication.

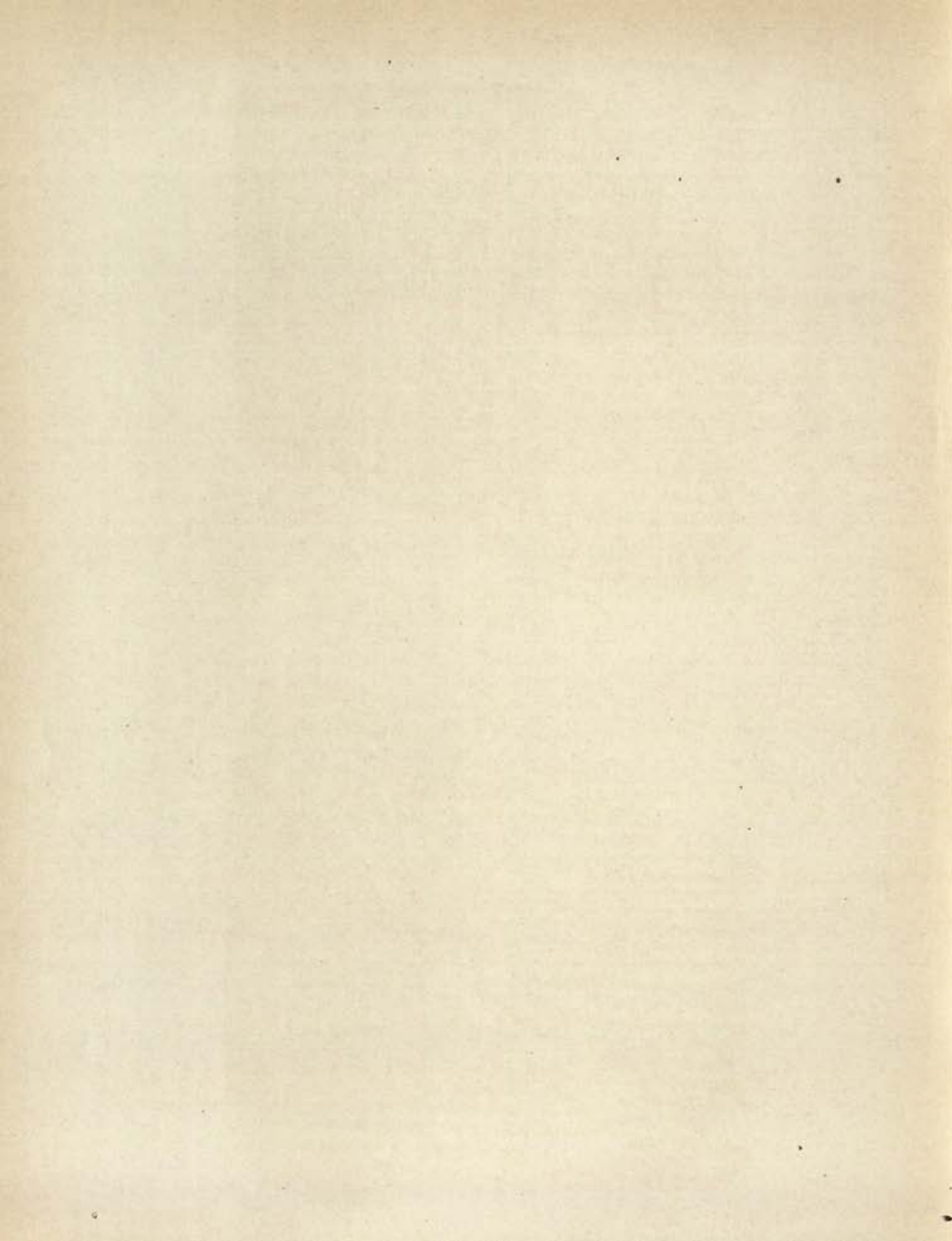
12. *Inanna and Enki or The Transfer of Civilization from Eridu to Erech*.—This is one of the largest and most significant myths in the entire group. It consists of eight hundred and nineteen lines, about six hundred of which are complete. It is reconstructed from the large text published by Poebel in HGT No. 25, from PBS I 1, No. 1 (a text whose copy is quite untrustworthy and which I have therefore carefully collated), and from an unpublished fragment discovered and copied by me in Istanbul, which supplies the motivating link in the story. Inanna goes to the Abzu in order to obtain for her city Erech the divine decrees governing the approximately one hundred cultural controls and objects which go to make up the warp and woof of Sumerian civilization. At a feast arranged for her by Enki, she succeeds in inducing him to present all the *me*, "divine decrees" to her; she loads them on the "Boat of Anu" and makes ready to depart for Erech. When Enki recovers from the effects of the banquet, however, he rues his munificence and decides to prevent Inanna from reaching

Erech. Seven times he attempts to have the boat and its precious cargo brought back to Eridu, but each time Inanna is saved by Anu's messenger Ninshubur. In spite of Enki's efforts she arrives in Erech safe and sound and is extolled and glorified by the people of the city for her feat.

13. *The Journey of Sin to Nippur*.—This composition consists of more than three hundred lines, more than half of which are complete. Sin journeys to Nippur with many gifts for his

father Enlil. He is welcomed by the latter who grants him in return all that is essential to the welfare and prosperity of Ur.

14. *The Marriage of Martu*.—Published by Chiera in SEM No. 58, this tablet is still unduplicated; neither in Istanbul nor in Philadelphia have I been able to locate any additional material. The myth, one of the most charming of the group, deals with the marriage of Martu to the daughter of Numushda, the main deity of Kazallu.



- PLATE I

Ni 368. obv.



CBS 9800. obv.

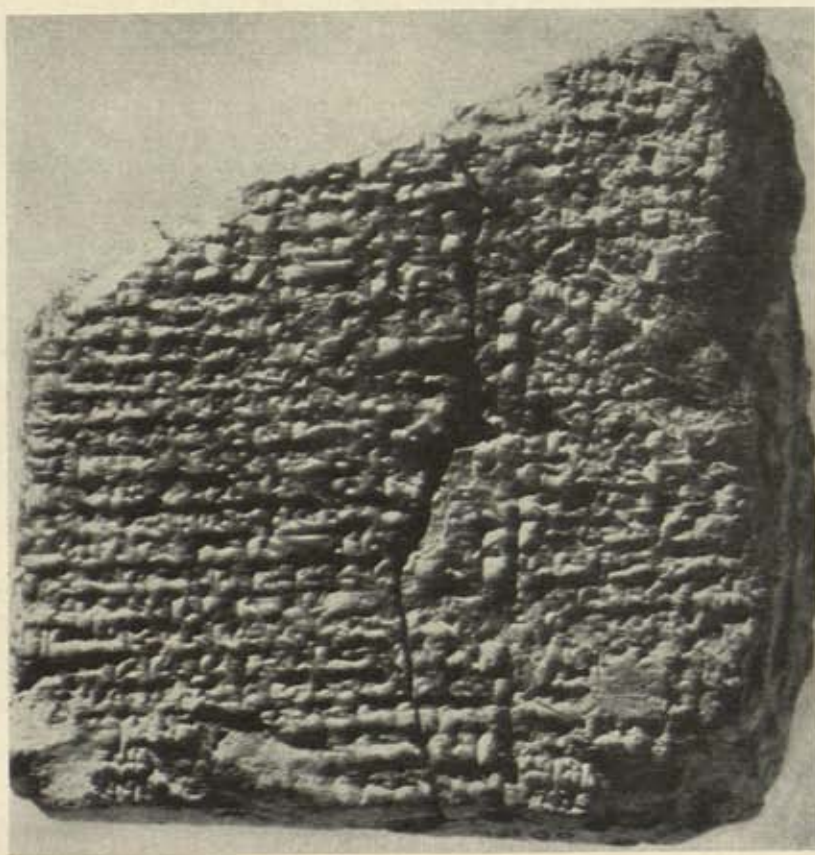


PLATE 2

CBS 9800. rev.



Ni 368. rev.



PLATE 3
CBS 13932.

obv.



rev.



PLATE 4

CBS 12368 + 12702 + 12752.

obv.



rev.



PLATE 5
CBS 13908.

obv.

rev.

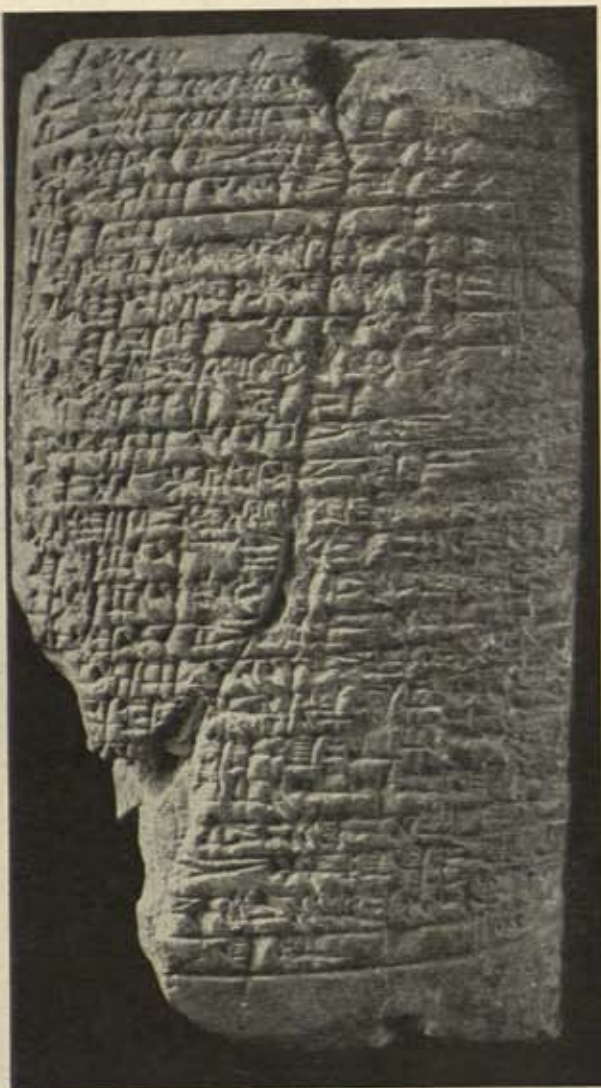
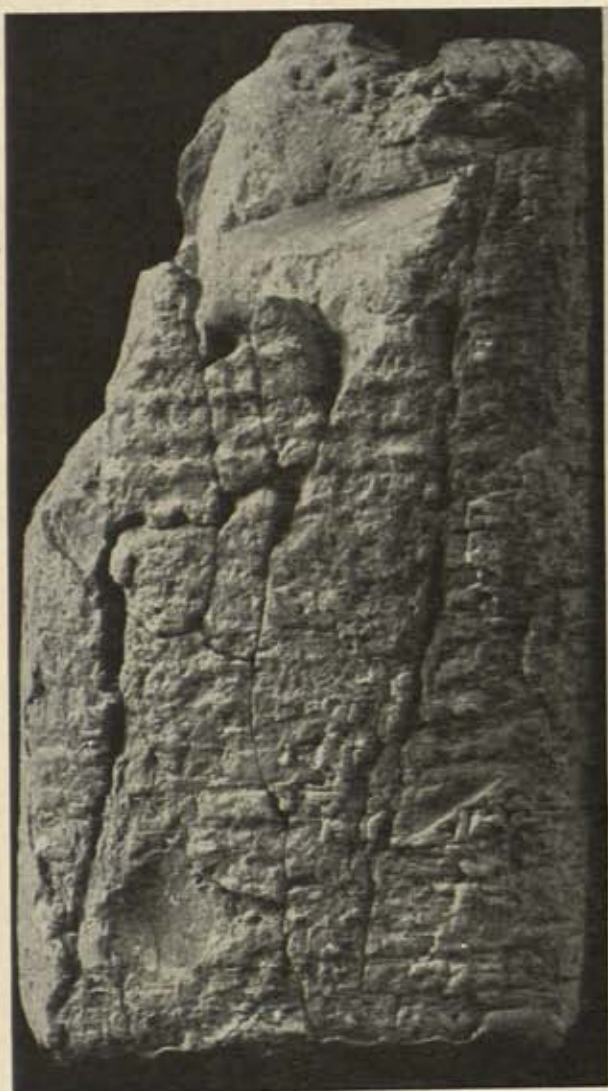


PLATE 6

CBS 11064 + 11088.

obv.

rev.



PLATE 7
CBS 15212.

obv.



rev.

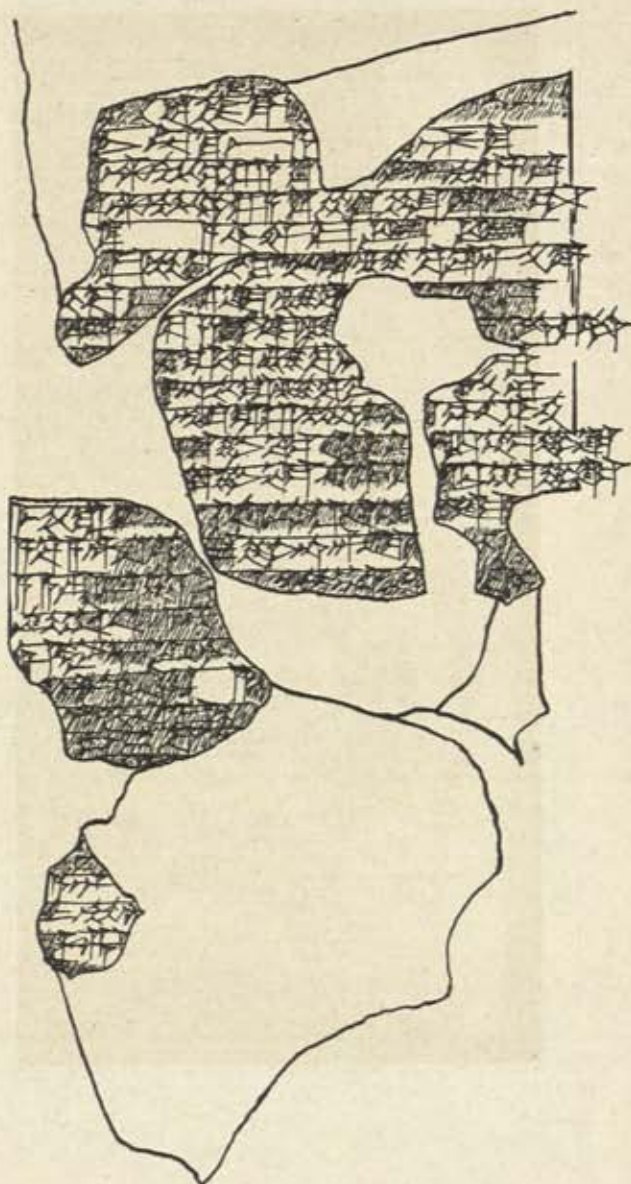
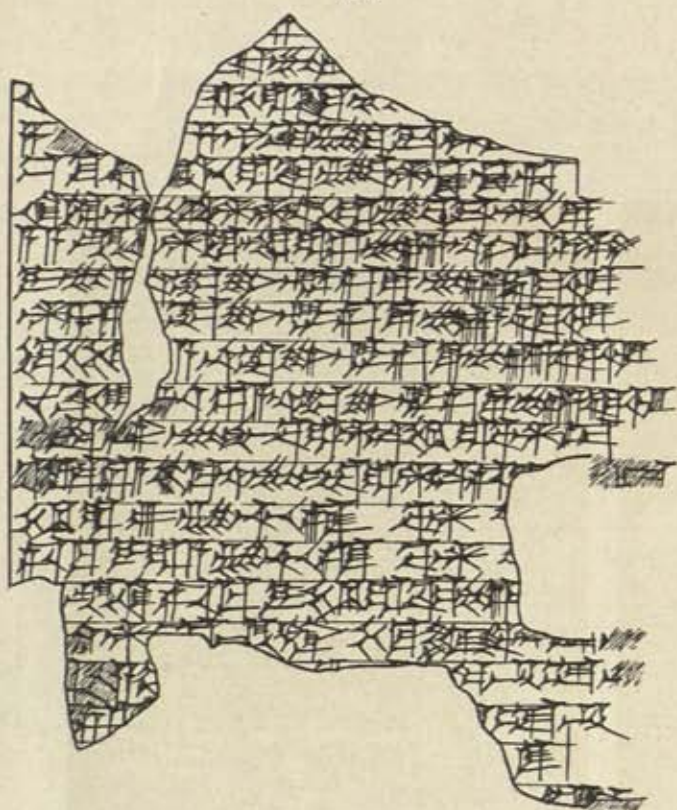


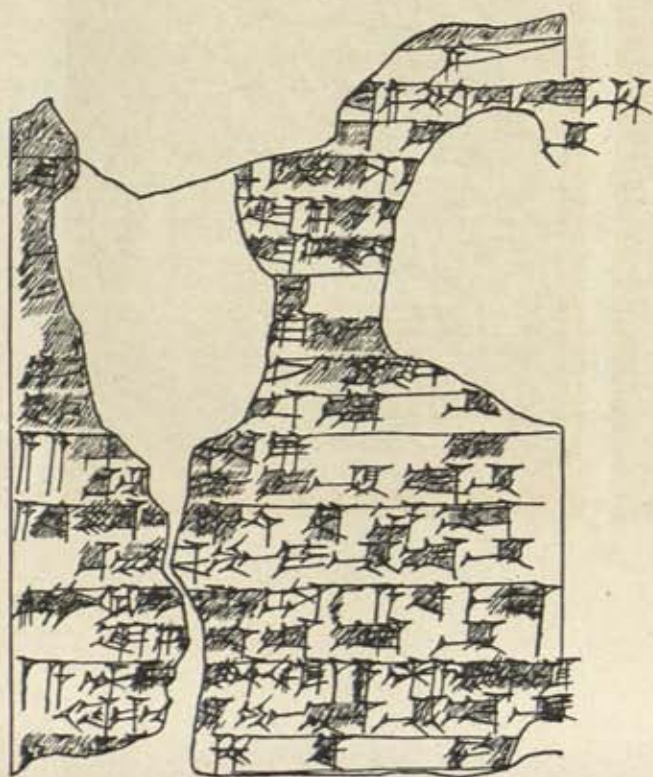
PLATE 8

Ni 4200.

obv.

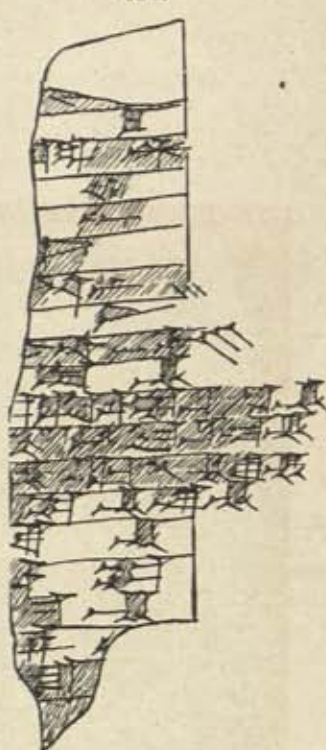


rev.



Ni 2762.

obv.



rev.

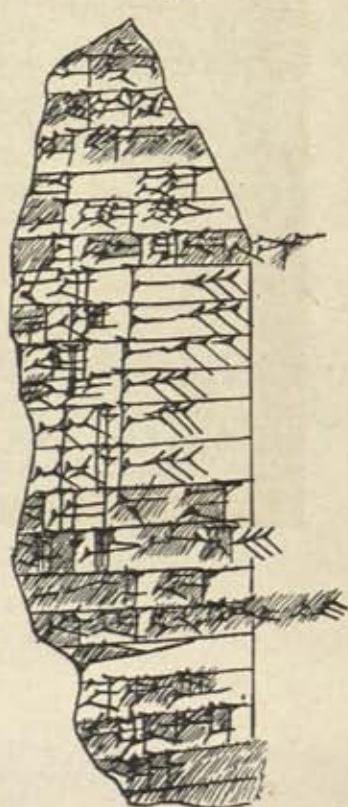


PLATE 9
CBS 13902.

obv.

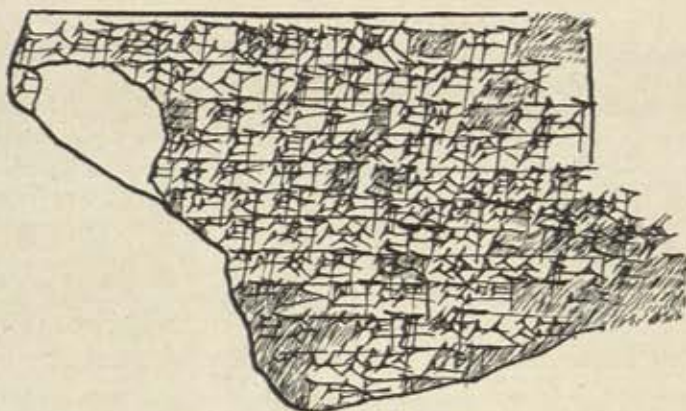
rev.



PLATE 10

CBS 15162.

obv.

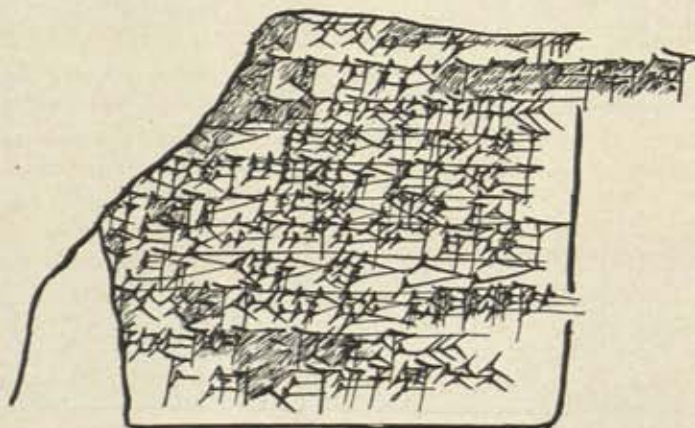


Ni 4034, obv.



rev. destroyed

rev.



A QUANTITATIVE STUDY OF THE PRODUCTIVITY OF THE FORAMINIFERA IN THE SEA

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ABSTRACT

Samples of populations of the foraminifer *Elphidium crispum* Linnaeus numbering from 500 to 1,000 individuals were taken both in the littoral and sublittoral zones of Plymouth Sound, Plymouth, England, at intervals of one month for 12 consecutive months. Percentage frequency distribution curves based on the number of chambers in the tests as determined from protoplasmic casts revealed that the life span in tide pools is usually one year, and the life cycle including a sexual and an asexual phase two years, while below low tide level two, three or even four years are required. Growth is limited to the spring and summer months and the rate of growth is 40 per cent greater and the diameter of the test 60 per cent larger in the sublittoral zone. Sexual and asexual reproduction as determined from the presence of juvenile individuals in the samples and cytological evidence of gametogenesis are limited to March and April, although some asexual reproduction takes place in the sublittoral zone in September. From the number of megalospheric juveniles produced in cultures and the ratio of microspheric to megalospheric individuals in the sea it was determined that the annual rate of increase is about thirtyfold and fortyfold in the littoral and sublittoral zones respectively. Populations well in excess of 1,000 individuals per sq. ft., were observed at a number of stations. In a later paper an attempt will be made to correlate these observations on the sequence of events in the life activities of this species with measurable ecological conditions in the sea.

INTRODUCTION

AN inspection of geological maps of the continents will reveal that rocks of marine origin cover approximately 70 per cent of the land areas. One of the principal biotic constituents of these rocks as well as that of recent marine sediments are the calcareous tests of foraminifera. Because of their universal distribution in ancient seas, the relative abundance, and the persistent nature of the calcareous tests, they provide a most useful guide in making stratigraphic correlations. In any attempt to comprehend the biological significance of the foraminifera in recent and geologic marine sediments we must consider the probable rate at which these tests have accumulated on the floor of the sea. This problem immediately calls forth such questions as: How numerous are living foraminifera in the sea? At what rate do they reproduce? What

is the life span? What factors influence the rate of growth? and What proportion of the tests are destroyed by organisms living in or above the sediments? Although there is a vast and growing literature on the foraminifera it contains virtually nothing that would contribute to a comprehensive solution of any of these problems (Cushman 1940).

Elphidium crispum Linnaeus (*Polystomella crista*), the species made classic through the work of Lister (1895) and Schaudinn (1903) on the life cycle is considered to exemplify best, this group of marine Rhizopods. Further geographical subspecies of *E. crispum* are to be found in all coastal regions, therefore this seemed to be the logical material for this first attempt to provide answers, based on actual observations, to the problems suggested above.

When foraminifera are killed, fixed, decalcified, stained and cleared, it is possible to note the size, arrangement, and total number of chambers. When chamber counts for samples of populations taken monthly for twelve months are plotted as frequency distribution polygons, much may be learned concerning seasonal variations in the rate of growth, reproduction, periods of dormancy, and the varying proportion of microspheric to megalospheric tests. The described methods also provided an abundance of material for cytological study.

For a statistical study of populations a dependable source of material is essential. In Plymouth Sound on the southwest coast of England *E. crispum* is abundant in two life zones. From small tide pools it was possible to take representative samples of the populations almost as readily as from a culture dish, and in the sublittoral zone equally representative samples were obtainable with the aid of a dredge from areas in which only slight variations in sediments and bottom configuration were observed. The population per unit area in these regions was determined from samples taken with a special suction grab, the number of living foraminifera in a sample being determined from the number of

protoplasmic casts that remained after the foraminifera had been treated with strong acidified alcohol.

The studies of Lister (1895) on the life cycle of this species were also made at Plymouth, and our observations of the activities of living foraminifera and permanent cytological preparations provide additional evidence in support of his work. Our results also explain in part why reported attempts to culture any but the smallest species of foraminifera have failed, and why the cytological behavior of the nuclei in division are so inadequately known.

Although our studies on *E. crispum* or its geographic subspecies extend over a period of ten years in the Pacific, the Atlantic, the Mediterranean, and the Java Sea, and during this time we have probably prepared for cytological study well in excess of 100,000 megalospheric individuals, many hundreds of which were in some stage of gametogenesis, we have failed to obtain evidence as to the fate of the relatively enormous nucleus that is characteristic of this phase of the life cycle. It is to be hoped that data on periods of reproduction contained in this paper will contribute to the solution of this fundamental biological problem, for in its solution depends to a major degree the ultimate fate of the chromidial theory of Hertwig which is now in a state of disrepute, but definitely has not been eliminated from consideration (Calkins 1933, p. 456, 236, and 87).

HYDROGRAPHIC CONDITIONS AT PLYMOUTH

Plymouth Sound on the southwest coast of England, has an average depth of 30 ft., and an extreme tidal range of 16 ft. Several streams with wide estuaries empty into the Sound and during periods of heavy rainfall these affect the salinity, particularly at the surface where it varies with each tidal phase and from season to season. The normal range of salinity is from 34.9 parts per thousand to 25.3 parts per thousand with an occasional low of 19.5 parts per thousand (Fig. 1). The mean monthly surface water temperatures vary from 16° C. in August to 8° C. in February. The estuaries and the deeper parts of the Sound have mud bottoms while on either side of the main channel the bottom is covered with quartz sand and small shell gravel. The abrupt rocky shores are fringed with dense growths of *Fucus*, *Lammi-*

naria, and other algae and the numerous tide pools on the reefs usually contain dense growths of *Corallina*.

As is typical in the higher latitudes, there is an abrupt and prolonged spring outburst of phytoplankton which soon depletes the nutrient salt content of the water. This is followed by several minor summer outbursts, and with the

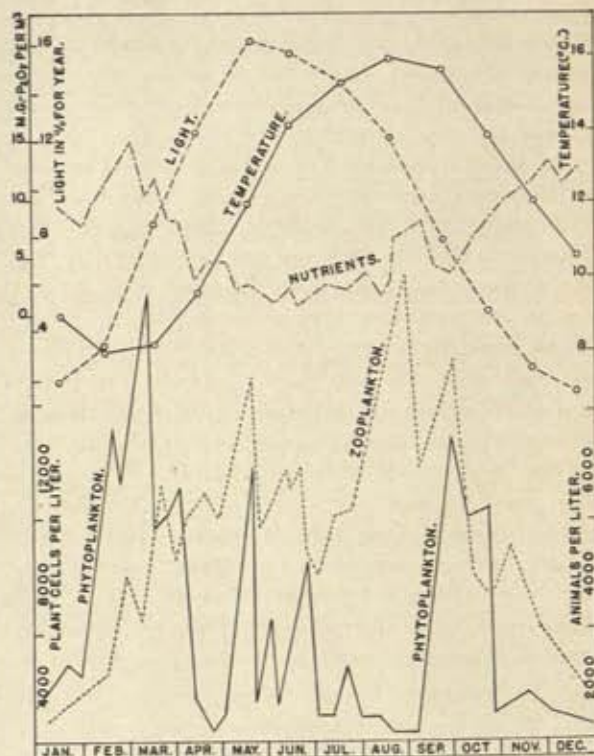


FIG. 1. Graphic presentation of conditions in the sea in the vicinity of Plymouth, England.

regeneration of the nutrient salt content of the water in the fall there is a second major outburst that is less intense and of shorter duration than that of the previous spring. Following the spring outburst of phytoplankton there is a rapid increase in the zooplankton population, and a more gradual increase extending into the fall. The reduced period of sunlight in the late fall limits the production of phytoplankton and there is a rapid reduction in the zooplankton population. The periods of growth and reproduction in the foraminifera are somewhat similar to those of the zooplankton and these life activities in both groups are no doubt related to the food organisms available in the microflora of the sea.

MATERIAL

From June 1938 to July 1939, a number of stations in the vicinity of Plymouth were worked monthly except at the height of the reproductive season in March and April when additional samples were taken. From several stations within Plymouth Sound enormous numbers of individuals were obtained with the aid of a dredge from a bottom composed of clean sand, shell fragments, and other neritic material, while smaller numbers were taken from tide pools containing a heavy growth of coralline algae both within the Sound and along the adjacent coast. Samples of sediments from the English Channel in the vicinity of Plymouth contained few living individuals of this species. The data for the frequency distribution curves presented in this paper were obtained from material taken in a small tide pool that was little more than a cleft in the rocks at about three-quarter tide level on the southeast side of Drake's Island, and dredgings from the sandy bottom north of the Island at from 5 to 7 meters below low tide level and only a few hundred meters removed from the tide pool station. Series of curves from other geographical regions will be presented in a later paper, and an attempt will be made to explain in part the influence of varying ecological conditions upon test morphology, growth, life span, periods of reproduction, and other life activities.

METHODS

Tide Pool Sampling.—*E. crispum* living on coralline algae, growing on the bottom and sides of small tide pools were obtained by removing handfuls of the algae including hold fasts and attached debris from representative areas within the pool. This material was then washed vigorously between the hands in a tubular sack, the bottom of which was a piece of silk netting having 2 mm openings and the top attached to a wooden ring that rested on the rim of a deep container filled with sea water. The sediments including the foraminifera were freed from silt and organic debris by repeated washing and decantation. Even when considerable care was used, some of the smaller foraminifera including two to four chambered *E. crispum* were lost. This loss, however, had only slight influence upon the frequency distribution curves of growth stages within a population, and no effect upon the interpretation.

Most plant and animal organisms living within the intertidal zone are better adapted to withstand several hours of slow desiccation than to remain in stale water for a much shorter period. For this reason when it was more convenient to prepare the material in the laboratory than at the collecting grounds the following procedure was adopted: The coralline algae were placed in a container which permitted the water that drained from the algae to escape, and the whole was then covered by larger algae in order to provide shade, and some cooling through evaporation. If the temperature in the container is not allowed to increase by more than a few degrees above the surface temperature in the sea, the foraminifera may remain for twelve hours or longer in a suitable condition for starting cultures.

Dredged Samples.—Dredgings were made with a one meter D-net, and when skillfully handled, samples consisting largely of surface sediments were taken. Much of the quartz sand which made up the bulk of these samples was dispensed with by placing several liters of the sample in a twelve liter container filled with sea water and then agitating the whole in such a manner as to cause the foraminifera, shell fragments, and other material of low density to collect at the surface of the heavier sand. This surface material including the foraminifera was then removed and washed as described in handling tide pool samples. By careful manipulation it was possible at times to obtain samples a liter of which contained several thousand *E. crispum*. Microscopic examination of the discarded sand usually revealed few foraminifera, and again it was of little consequence that a few of the earlier developmental stages were lost.

Unit Area Samples.—Population counts were made from samples of sediments taken with a Hunt Suction Grab Sampler (Hunt, 1926-27). This grab consists of a compression chamber provided with a delivery tube that empties into the upper portion of the chamber, and is closed at the lower end by a glass disc. The glass disc is held in place by heavy grease and a tubular brass sleeve provided with ports in which the smaller end of a funnel-shaped sampling device slides freely in such a manner that the ports are closed when the grab strikes the bottom, and at the same moment a plunger smashes the glass disc. The air in the chamber is compressed by the inrush of a watery sample of bottom sediments driven through the delivery tube into the

chamber at a pressure that is equal to the weight of the column of water above the bottom. As the grab is hauled to the surface the sample is not subjected to washing, nor can it otherwise escape as so often happens with many sampling devices when there is an appreciable amount of shell fragments and other coarse material in the sediments. The surface sample of sediment taken is three inches in diameter and when the grab is used in deeper water the volume of the sample may be controlled by placing an amount of water in the chamber that is equal to the difference between the volume of the sample desired and the volume of water that would enter the chamber at a particular depth. After the sample is removed it is washed in a tubular sack made of No. 25 bolting silk that retains the smallest foraminifer, and at the same time allows the escape of clay and silt particles. From samples so taken it is possible to estimate the population per unit area on the floor of the sea by determining the number of living foraminifera in the sample after treating it with a 10 per cent solution of formalin at 65° C., and then counting the protoplasmic casts that remain after the calcium carbonate of the tests has been removed with acidified alcohol.

Cytological.—Paraffin sections and total mounts were made from material fixed in Schaudinn's fluid at 65° C., although equally satisfactory results were obtained by first killing in hot water at 65° C., and then adding sufficient formalin to make a 10 per cent solution. The foraminifera were separated from other sediments in 70 per cent alcohol with the aid of a low power binocular microscope using 4× oculars and 8× objectives. Much time was saved by using a sorting chamber made from a 10 cm petri dish, the bottom of which had been marked with a diamond pencil into parallel lines so that the distance between two lines was a little less than the diameter of the field of the microscope. Only sufficient sediment was placed in the dish to cover the bottom with scattered particles, so that few foraminifera would be covered with other objects. By using the parallel lines as guides it was unnecessary to inspect the same areas a second time except in a superficial manner. The foraminifera were removed from the sorting chamber with a mouth controlled pipette and were transferred to a 5 cm syracuse watch glass. Decalcification of the tests was accomplished in 85 per cent alcohol to which sufficient hydrochloric acid had been added to cause bubbles of carbon dioxide to form

slowly on the walls of the test, then immediately adding neutral alcohol to stop all effervescence. This step should be carried out in a comparatively large volume of alcohol and should not be completed in less than twelve hours or there is danger of destroying the relationship of the chambers and the canal system.

Ehrlich's Acid Haematoxylin proved a suitable stain for total mounts, although when material was to be prepared as thin sections they were stained in alcoholic Eosin. The latter stain has a strong affinity for the plastin in the nuclei of foraminifera and should be differentiated in acidified alcohol in the same manner as when using Ehrlich's Haematoxylin. After clearing it is possible to select those individuals which show evidence of reproductive activity or other characteristics that make it desirable that they be sectioned. Heidenhain's Iron Haematoxylin was used on sections.

Foraminifera used for population studies were decalcified, stained, and cleared in clove oil and the number of chambers in each individual determined without removing the foraminifera from the original container. This is necessary since several of the distal chambers are often devoid of cytoplasm and the delicate chitinous lining of these may be easily lost.

THE LIFE CYCLE OF *Elphidium crispum*

In the life cycle of *Elphidium crispum* as proposed by Lister (1895) there is a cyclical alternation of sexual and asexual generations. This alternation of generations results in two types of individuals which cannot be recognized from external characters except in the earliest stages, but the morphological beginning and cytological organization of both are distinguishable at all times, see Plate I.

In the sexual phase, biflagellated gametes associate in pairs in fertilization and the resulting zygotic amoebula becomes invested in a calcareous test. Subspherical and later crescent-shaped chambers are added to this initial chamber one at a time in ever increasing size to form a bilaterally symmetrical involute spire. Immediately following fertilization there is a rapid increase in the number of nuclei so that the sexually produced agamont generation is multi-nucleate from the earliest observed stage.

Prior to asexual reproduction a second period of nuclear division takes place. The protoplasm and contained nuclei then escape from the test

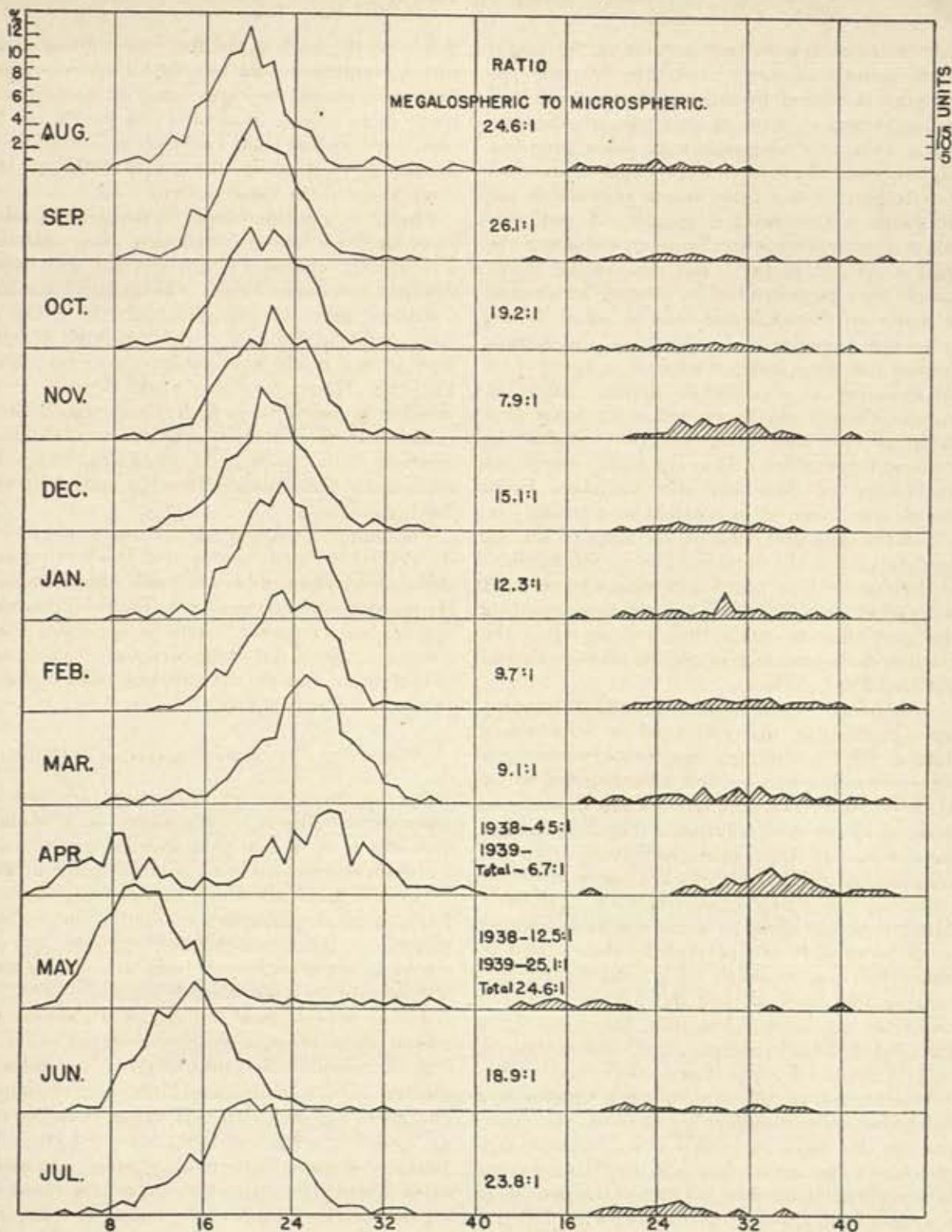


FIG. 2. Frequency distribution curves of growth stages in terms of the number of chambers in 500 *E. crispum* taken at monthly intervals for 12 months from a tide pool on Drake's Island. Curves for the megalospheric agamonts are based on percentage frequency distribution for each class, while the actual number of microspheric agamonts in the sample is represented. The changing ratio of microspheric to megalospheric individuals in April and May followed by the occurrence of juveniles of the respective generations show that the period of reproduction is brief, that the life span is one year and that two years are required to complete the life cycle.

and multiple fission of the somatella results in as many ameobulae as there were nuclei present. The single nucleus of these asexually produced individuals does not divide during vegetative life. Since these amoebulae have a diameter in excess of five times that of the zygotic ameobulae, there is a corresponding difference in the relative size of the initial chamber or proloculus of the tests of the two generations and these are referred to as the megalosphere and microspheres respectively, and with the addition of chambers megalospheric and microspheric tests. In megalospheric tests only the proloculus is spherical all other chambers being crescentic in shape.

In the mononucleate megalospheric gamont, gametogenesis begins with a rapid increase in the numbers of nuclei with a corresponding diminution in size. Multiple fission of the somatella in this generation takes place within the test and results in mononucleate gametocytes. A final nuclear division which is immediately followed by binary fission of the gametocyte results in subspherical gametes which become biflagellated. These gametes soon escape from the tests and become free and pelagic. It is probable that fertilization takes place between gametes derived from different individuals soon after their release, as was described by Schaudinn (1903). In both phases of the life cycle reproduction terminates the existence of the individual.

THE LIFE SPAN

When the number of chambers in each of 500 megalospheric *E. crispum* taken at monthly intervals from a tide pool were plotted for each month as frequency distribution polygons, the resulting curves were nearly normal except for the month of April when a bimodal curve indicative of a second megalospheric generation was obtained (Fig. 2). The virtual elimination of what had been the major portion of the population in March, together with the appearance of enormous numbers of juveniles in May made

it evident that the life span of this phase of the life cycle is one year. A similar series of curves for the microspheric generation made it equally evident that the life span of this second phase of the life cycle is also one year, and that two years are required to complete the life cycle.

A series of samples of one thousand individuals from the sublittoral zone were used in a similar study (Fig. 3). These larger samples were desirable because of the wider limits in the numbers of chambers, e.g., 80 as a maximum compared with 40, and the smaller ratio of microspheric to megalospheric individuals, or 1 to 38 compared with 1 to 25 in tide pools. In this second group of curves a bimodal condition exists for most months, both for microspheric and megalospheric individuals, and it is evident that the two major modes represent different generations. The maxima extremes for the numbers of chambers in individuals from this life zone do not change appreciably throughout the year, but in the series of curves for the megalospheric generation there are two minima modes, the major coming in May and the minor in October. The juveniles produced in the fall failed to survive the winter so that the only influence on the population was to decrease the ratio of microspheric to megalospheric individuals the following spring. No cytological or other evidence was observed that would suggest a corresponding period of sexual reproduction in the fall. As was stated, the curves for May through August are bimodal, but in September the more rapid growth of the juveniles compared with the rate of growth in those surviving from the previous generation resulted in the overlapping of the two curves, so that the curves for October to May had but a single mode. A bimodal curve was again obtained in May, and it is evident that the first mode represents individuals produced in the spring, while the second represents those that had failed to reproduce, and would therefore be two years old the following spring. Microspheric individuals were so in

FIG. 3. Frequency distribution curves of growth stages in terms of the number of chambers in 1,000 living *E. crispum* taken with a dredge at 5 to 7 meters north of Drake's Island. The smaller monthly samples obtained during the period of winter dormancy were treated as a composite sample. The occurrence of vast numbers of megalospheric juveniles in May and a smaller number in October show that there are two periods of asexual reproduction, while cytological preparations made it evident that sexual reproduction takes place in March and April only. The bimodal curves for the megalospheric phase in May, June, and August represent at least two generations that were produced in different years and suggest that larger individuals are at least two years old. The same is true of the microspheric generation so it is evident that the life span for the respective generations is at least one year, and that two, three or four years are required to complete the life cycle in this life zone. For comparison curves for the tide pool populations from the adjacent foreshore are represented in broken lines. Stippled area in the curve for March represents that part of the population showing some phase in gametogenesis.

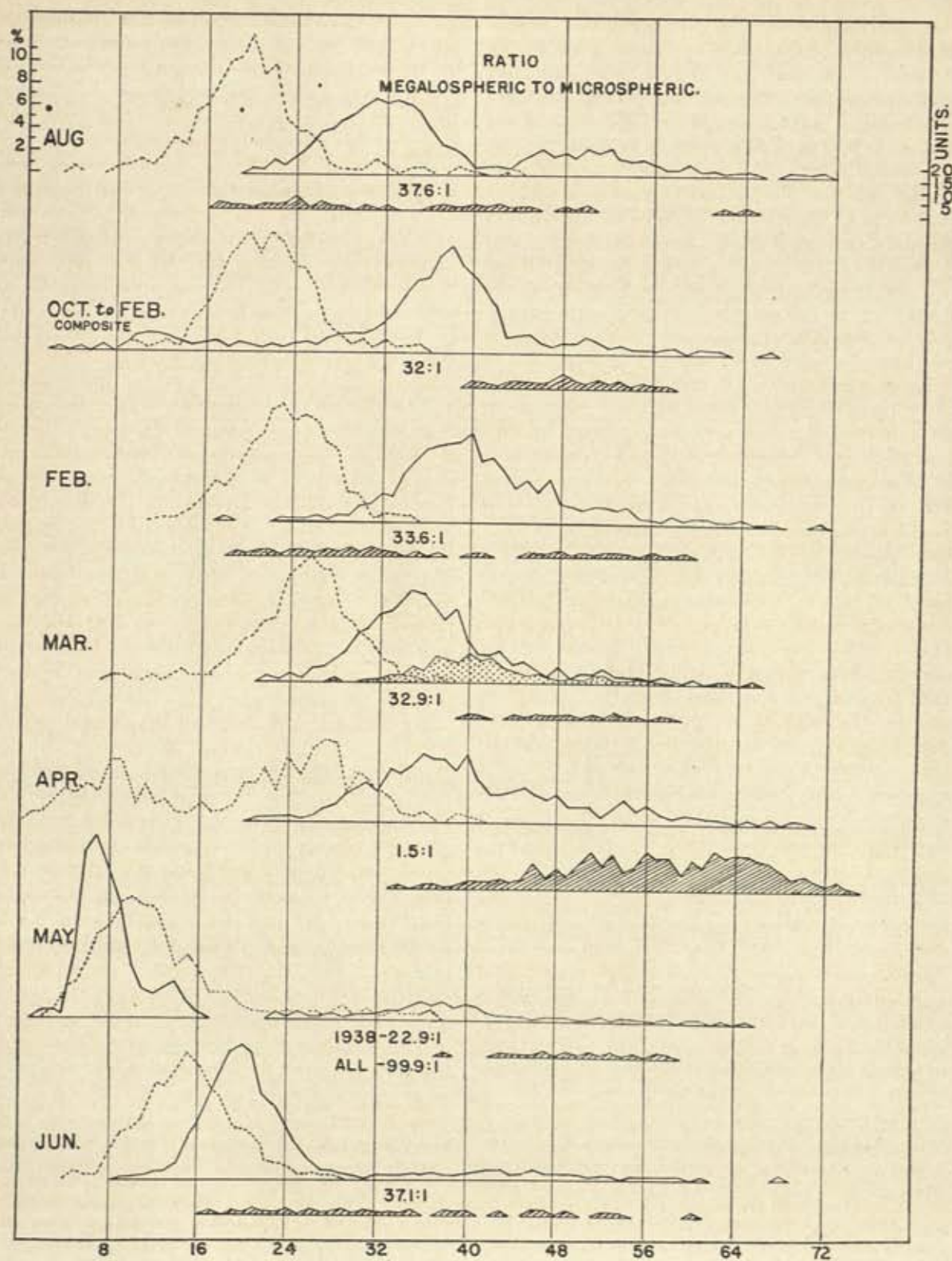


FIG. 3.

the minority and the limits in numbers of chambers such, that the curves for this phase of the life cycle are somewhat more difficult to analyze. One of the most significant features of the series is the enormous increase in the ratio of microspheric to megalospheric individuals in April, and the return to the more normal ratio one month later. Since we know that reproduction terminates the existence of the individual this abrupt change can have but one explanation and that is that sexual reproduction in the early spring had resulted in the elimination of most of the megalospheric gamonts that were then either one or two years old, and that later asexual reproduction by a similar proportion of one and two year old microspheric agamonts resulted in the restoration of approximately the former ratio.

Since the life span of megalospheric *E. crispum* living in the sublittoral zone is either one or two years, and the maxima extremes in numbers of chambers are similar in both generations, it follows that the life span of microspheric individuals is also one or two years, and the life cycle including a sexual and an asexual phase requires two, three or even four years.

In the sublittoral zone, sexual reproduction by megalospheric gamonts precedes asexual reproduction by microspheric agamonts by approximately one month, therefore microspheric individuals are produced one month earlier in the spring and survive one month longer the following spring and therefore have a life span that is approximately two months longer than that of megalospheric individuals. This explains in part the larger size of microspheric tests found in the sediments. In the tide pool the difference in the life span in the respective generations is only about one-half that observed in the sublittoral zone or from three to four weeks.

The life span of *E. crispum* is perhaps longer than that of most foraminifera living in the same life zones. In our experience with cultures we found that under the most favorable conditions *Discorbis globularis* (d'Orbigny) produced a test having nineteen chambers in fifty-two days. Microspheric *Patellina corrugata* Williamson, which is the form usually recovered from the sediments, matures in twenty-one days, while microspheric *Spirillina vivipara* Ehrenberg matures in only ten days, but in the sea, the nature and size of *S. vivipara* suggests that the usual life span is several times this.

RATE OF GROWTH

Winter is a period of dormancy, more as a result of food shortage than of low temperature. This is suggested by the fact that the period of greatest growth and reproductive activity immediately follows the month of lowest temperatures for the year, e.g. February, and the excessive shrinkage of the protoplasm observed in material taken in the late winter and early spring which had been prepared by cytological methods that had not produced shrinkage at any season at La Jolla, California, or throughout the summer and fall at Plymouth, England, (Pl. I, Fig. 8). In March there was a gradual refilling of the chambers beginning with the distal and later extending to the earlier formed chambers. In dredged samples taken north of Drake's Island on February 14, when the water temperatures were minimum for the year, renewed activities of the foraminifera had already resulted in the filling out of the distal three to fourteen chambers, and in 52 individuals in a sample of 1,133, or 4.5 per cent all chambers were filled. One month later on March 14, 386 in 1,155 or 33.4 per cent showed little shrinkage, and the remainder were rapidly filling. This individual difference in the time when activities were resumed depended to some extent upon the time water turbulence disturbing the bottom sediments uncovered the foraminifera that had been buried as a result of turbulence earlier in the season, and how soon they were able to avoid becoming reburied to a depth from which they were unable to escape, a depth that does not exceed 5 to 8 times the diameter of the test, or for large individuals about 1 centimeter.

A sample taken from a tide pool on Drake's Island on March 14, contained only 126 in 500 individuals or 25.2 per cent in which the tests were filled with protoplasm, while the remainder still showed considerable shrinkage. This was 8.2 per cent lower than was observed in a sample taken in the sublittoral zone on the same date. This was unexpected for in the tide pools the foraminifera were free to begin feeding and growth activities as soon as conditions became favorable.

The rate of growth in a population as determined from the mean rate at which chambers are added to the tests is more dependable than linear measurements of the tests, although satisfactory results could be obtained through the use of curves based on measurements of ground

sections of tests (Fig. 4). Chambers added in the early spring are wider, longer, and thicker than those produced during the late spring and summer, and especially the final chamber or two

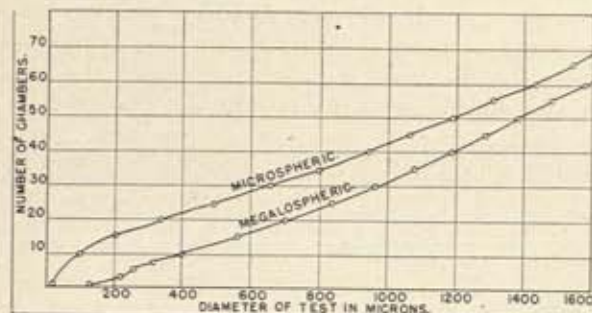


FIG. 4. Curves based on measurements of ground sections of tests of *E. crispum* taken in the sublittoral zone. The mean, maximum diameter of 10 microspheric and 10 megalospheric tests were determined by measuring across the sections at 5 chamber intervals.

produced in the late fall when activities resulting in growth were at a minimum. This usually results in a depression in the outer margin of the test. For these reasons it is possible to determine the number of new chambers added after the resumption of growth in the spring, and in succeeding samples, the rate of growth.

Thus, on March 20, larger individuals from dredged samples averaged 3.2 new chambers, April 29, 5.5, May 12, 9.1, and June 15, 14.7 which was an average of one chamber in 5.9 days. In these large individuals the time required to produce a new chamber, including the secretion of a delicate membranous cyst that partially encloses the test and makes it fast to the substratum, the absorption of water to increase the volume of protoplasm causing the extrusion of a mass of hyaline ectoplasm that gives shape to the developing chamber, and the secretion of the calcareous walls requires from 12 to 18 hours, as was determined from cultures. In the five days remaining, the foraminifera must acquire, digest, and assimilate sufficient material with which to produce the succeeding chamber. At first the rate of growth in tide pool populations was somewhat greater than that observed in populations from the sublittoral zone. This was due in part to the shorter interval between the addition of successive chambers in these smaller individuals.

The data on the rate of growth throughout the late spring and summer are more complete for the megalospheric than for the microspheric gen-

eration because of the prevalence of the former in the population, and it is also possible to take large numbers of megalospheric juveniles from the earliest stage whereas it is unusual to take microspheric juveniles before the test consists of 12 chambers because of their smaller size, e.g., the average megalospheric proloculus has a diameter that is about equal to that of the test of a microspheric juvenile having ten chambers, and has several times the mass.

Growth curves based on the mean number of chambers in tests show that by September 15, the average megalospheric individual living in a tide pool had developed 20 chambers and had a diameter of 430 μ , compared with 28 chambers and a diameter of 380 μ for microspheric individuals (Fig. 5). In the sublittoral zone the average megalospheric test on the same date had 33 chambers and a diameter of 1,040 μ and microspheric tests, 47 chambers and a diameter of 1,100 μ . Therefore the rate of growth in numbers of chambers was about 40 per cent more and the diameter of the tests 60 per cent larger in *E. crispum* living in the sublittoral zone

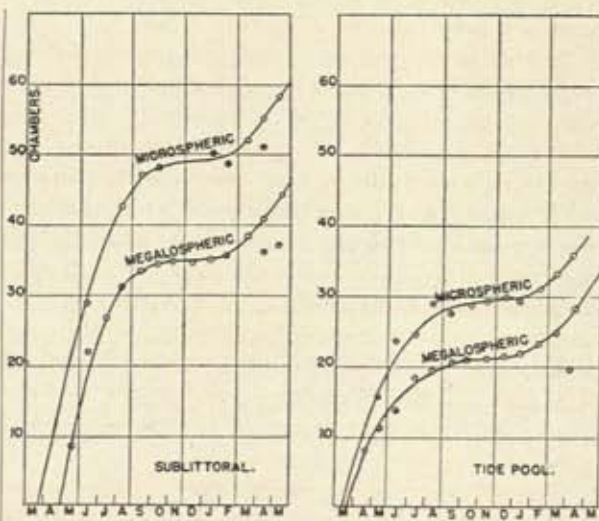


FIG. 5. Growth curves for *E. crispum* obtained by plotting the mean number of chambers in samples taken at monthly intervals. Open circles indicate the mean number of chambers added in the spring of the second year rather than the mean number of chambers for all individuals.

than in those from the littoral zone. In Fig. 6 it will be noticed that the least diameter for megalospheres in individuals taken in the sublittoral zone is larger than the mean diameter for the class of those taken from the tide pools. Similar growth differences have been observed

by us in other species of foraminifera which inhabit these two life zones although there are those, who, with some justification, would regard the two forms as distinct species and it is

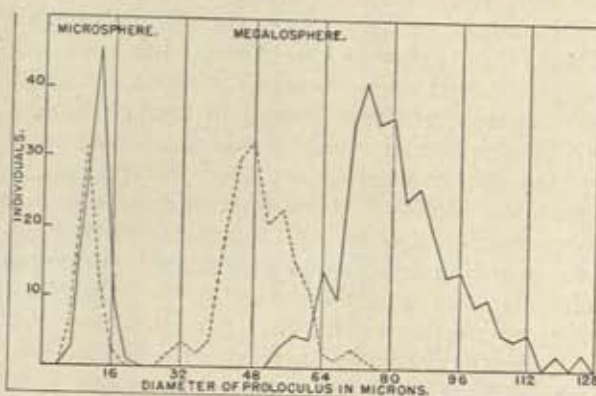


FIG. 6. Frequency distribution curves for the mean diameter of the proloculus of *E. crispum*. Broken lines represent 50 microsphere and 218 megalospheric individuals from tide pools and solid lines 82 microsphere and 352 megalospheric individuals from samples taken in the sublittoral zone.

true that in larger and more complex invertebrates where specific differences are more easily recognized, closely related forms do co-exist.

One example is the common bay mussel *Mytilus edulis* Linnaeus which is most numerous in the intertidal zone, while along the coast of California the larger *Mytilus californianus* Conrad thrives immediately below low tide level. In the case of *E. crispum* Mr. Arthur Earland is agreed that we are probably dealing with a single species and that the observed differences were the result of the conditions under which they were produced.

Data in addition to those presented in Figs. 1 and 2 were used in preparing the growth curves in Fig. 5.

PERIODS OF REPRODUCTION

The approximate dates for the beginning and ending of the reproductive activities can be determined from several sources. These sources include cytological evidence of gametogenesis in the megalospheric generation, Pl. I, Figs. 6 and 7, nuclear division in microspheric individuals which immediately precedes asexual reproduction, the increasing and diminishing ratios of microspheric to megalospheric individuals in a population (Fig. 7), the number and position of modes in frequency curves for the respective

generations (Figs. 2 and 3), and finally the rate of growth in each of the two generations (Fig. 3). From these data we have concluded that in 1939 *E. crispum* living in the littoral zone produced sexual gametes from March 14 to April 18, and that the probability of finding gametes after the latter date was only one in many thousands. Asexual reproduction beginning about March 24 was nearly 60 per cent complete by April 22, although it continued at an ever diminishing rate until July 15, when few mature microspheric individuals remained. It is true that an occasional microspheric individual asexually produces megalospheric juveniles whenever conditions become suitable, but the rare occurrence of megalospheric juveniles having less than 8 chambers after May 15, suggests that it would be most unusual to observe cytological or other evidence of asexual reproduction throughout the summer, and that cultures started at this time

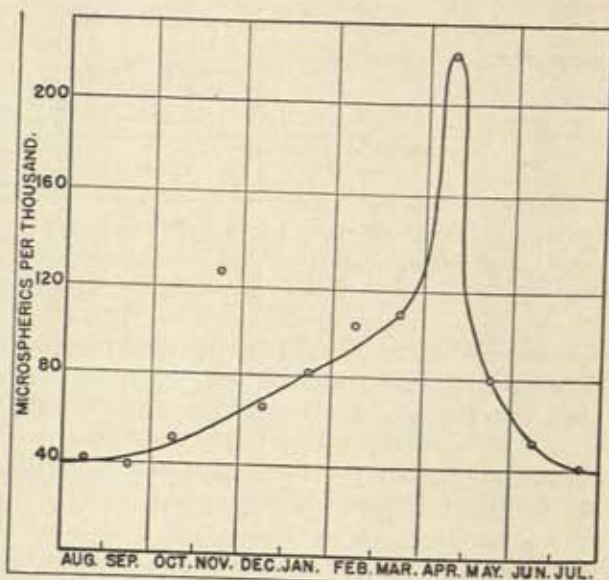


FIG. 7. Seasonal change in numbers of microspheric agamonts per 1,000 individuals in tide pool populations of *E. crispum*. The abrupt increase in the proportion of microspheric to megalospheric individuals in April resulted from a reduction in the number of megalospheric gamonts due to sexual reproduction in March and was followed by an equally abrupt decrease in the proportion of microspheric agamonts in April following asexual reproduction.

of the year would probably fail to produce evidence of either sexual or asexual reproduction for some months.

In the sublittoral zone the period of sexual reproduction extended from March 14, to April

22, and the probability of obtaining cytological evidence of this type of activity after May was again negligible. Asexual reproduction in this life zone was somewhat later and may be associated with the rate of recovery from winter dormancy of the relatively enormous multinucleate microspheric individuals in which the mean number of chambers was 58 compared with 36 for microspheric individuals living in tide pools, although in the sexual phase of the life cycle it was observed that in a population the larger megalospheric individuals reproduced earlier. Judging from the first appearance of the megalospheric juveniles in the sediments of the sublittoral zone asexual reproduction by microspheric individuals began about April 6, and continued until May 30, although an occasional individual may reproduce during the summer. In October megalospheric juveniles were again numerous and from the observed rate of growth and the absence of juveniles in the previous samples it would seem that these had been produced soon after September 15.

RATIO OF MICROSPHERIC TO MEGALOSPHERIC INDIVIDUALS

The ratio of microspheric to megalospheric individuals is of interest to the taxonomist because descriptions of both phases of the life cycle are desirable. These descriptions are usually made from ground sections, and it is often necessary to make tens or even scores of preparations to find a microspheric test. The ratio of these two forms within a given species is roughly similar in most regions, but in a population the ratio varies according to the season, and with the substratum upon which they live.

One hand full of coralline algae from a tide pool may show a ratio of microspheric to megalospheric individuals of 1 to 10, and a second hand full from a different part of the same pool, a ratio of 1 to 25. This difference in ratios is probably related to the amount of protection afforded in the respective areas. Throughout the growing season the mean ratio remained 1 to 25, while in the sublittoral zone where there was less protection, the ratio was little more than one-half this, or 1 to 37. In the sediments of the sublittoral zone the ratio of microspheric to megalospheric tests average about 1 to 40, while in the foraminiferal population the ratio from March to September, which is the principal growing season, is about 1 to 37. During a brief

interval following the period of asexual reproduction by the megalospheric generation in late April, the ratio was 1 to 2.1, and in one sample 1 to 1. On a mud bottom a ratio of 1 to 99 was obtained as late as June due probably to the failure of the sexual phase of the life cycle in this habitat. In May at the close of the period of asexual reproduction a ratio of about 1 to 37 was resumed in the area north of Drake's Island.

It was stated that in tide pools the ratio during the growing season was about 1 to 25. After the period of sexual reproduction was well advanced, a ratio of 1 to 4.5 was observed, while one month later when asexual reproduction was virtually complete the ratio was 1 to 24.6.

From the above we may conclude that although the ratio of microspheric to megalospheric tests in the sediments remains relatively constant, the ratio in living foraminifera in a population varies within wide limits.

The frequency distribution curves for the mean diameter of the proloculus of microspheric and megalospheric tests from the respective life zones (Fig. 6), are based on measurements of material prepared for cytological study in which some shrinkage had taken place, but since all material was prepared in the same manner any slight error would remain constant for all individuals. From these curves it will be observed that there is a distinct size difference in the two generations as has been generally accepted. This, however, is not the case in all genera, and it is often necessary to use other characteristics such as the shape of the proloculus and the succeeding chambers, the ultimate size and shape of the test, or to note the number of nuclei. In general it may be stated that in most species the small proloculus of the sexually produced microspheric generation is nearly spherical and that many nuclei are to be found in the cytoplasm (Myers, 1940).

RATE OF REPRODUCTION

Since reproduction terminates the life of the individual, the rate of reproduction depends upon the number of juveniles produced and the length of the life span. From growth curves we have determined that the life span of *E. crispum* in tide pools is one year. At La Jolla, California, we observed that the number of progeny asexually produced by microspheric individuals removed from tide pools ranged from 52 to 128 with an average for 20 groups of 119, and from the number of nuclei in microspheric agamonts from Plymouth Sound it would seem that this

rate was about equal in the two regions. In sexual reproduction each megalospheric individual produces several thousand gametes. The probability of two gametes uniting in fertilization and the chance of the resulting zygote surviving to a stage where it may be readily recovered from the sediments can be estimated from the ratios of microspheric to megalospheric individuals observed before and after the period of reproduction. These ratios were found to be about 1 to 10 and 1 to 25 respectively. Since microspheric and megalospheric individuals were produced in the ratio of 1 to 25 and the actual number of megalospheric juveniles asexually produced by a microspheric individual was 119, then, individuals of the two generations were actually produced at a ratio of about 4.8 to 119. Prior to reproduction there were ten times as many megalospheric as microspheric individuals, therefore 10 megalospheric individuals produced the equivalent of 4.8 microspheric juveniles, or in other words the gametes from 2.1 megalospheric individuals were required to produce 1 microspheric juvenile that survived to develop a test having ten or more chambers. If 1 microspheric produces 119 megalospheric, and 2.1 megalospheric 1 microspheric, then the annual rate of productivity for the two generations is about fortyfold.

Reproduction was not observed in microspheric individuals taken in the sublittoral zone, but the rate of reproduction may be determined from cytological preparations of individuals about to reproduce, or which were reproducing when killed and fixed. A microspheric individual about to reproduce may be recognized in several ways. Often there is a remnant of a delicate protective cyst clinging to the test composed of animal cement, fragments of diatom frustules and other debris, the protoplasm usually has receded from the inner whorl of chambers and there is evidence of nuclear division or an unusual number of large nuclei of approximately the same diameter, suggesting that most of the nuclei have divided at least once, and that nuclear division was followed by growth of the daughter nuclei. The number of nuclei in microspheric individuals about to reproduce was found to be from 152 to 224 whereas the usual number was 27 to 52. Since the ratio of microspheric to megalospheric individuals in the sublittoral zone before and after the period of reproduction is about 1 to 33 and 1 to 37 respectively, and if we assume that the average

number of megalospheric juveniles produced by one microspheric individual is 200, then by the same computation discussed above, we may deduce that 6 megalospheric individuals are required to produce a single microspheric juvenile, and that the rate of increase for the two generations is about thirtyfold, compared with fortyfold for *Elphidium crispum* living in tide pools. From the ratios of microspheric to megalospheric individuals in the two life zones it is evident that sexual reproduction is more successful in tide pools where more protection is afforded and circulation is reduced for long periods between tidal phases.

POPULATION PER UNIT AREA

No attempt to distinguish between species of foraminifera which constitute a population from a mere assemblage of tests nor to determine the population of foraminifera on the floor of the sea has come to our attention.

Three samples taken with the Hunt Suction Grab on February 16 north of Drake's Island at a depth of about 7 meters contained 4, 7, and 12 living *E. crispum* respectively, while a similar sample taken on June 15, contained 40, 58, and 62, or approximately five times the number taken in February. Since the grab takes a surface sample 3 inches in diameter, the maximum number of *E. crispum* per unit area observed that had survived the winter was equal to 245 individuals per sq. ft., while the maximum population observed which was in June was 1,225 per sq. ft. This was the greatest population per unit area for this or a comparable species observed by us except in the coral reef areas of the Java Sea. Counts of living *E. crispum* may be easily made because the bright greenish brown color of the protoplasm shows through the walls of the test, while empty tests are either translucent or chalky white depending upon how long the organism has been dead. These counts, however, were later substantiated by decalcifying the foraminifera and determining the number of protoplasmic casts that remained. This step was necessary in making population counts of most species living on mud bottoms where the tests become filled with a precipitate of aluminum silicate, and it is necessary to use biological stains to differentiate living from dead foraminifera.

The determination of the population per unit area in tide pools would have little significance

because of the variable nature of the habitat especially in the small pools that proved so useful for other studies, nor would a comparison of the numbers of foraminifera per unit volume of the sediments from the two life zones contribute appreciably to this problem since the samples were taken by different methods. A comparison, however, is interesting for other reasons. A tide pool sample of washed sediments taken on July 15 contained 91 *E. crispum* per cc, while a similar amount of washed sediment from the sublittoral zone taken on the same day contained 126 individuals of the same species. Tide pool foraminifera remained fairly numerous throughout the winter, although it was necessary to examine much larger amounts of washed sediments to obtain the 500 *E. crispum* desired.

From March to October samples of sediments from the sublittoral zone contained more *E. crispum* per cc than were to be found in half a liter from October to February. In February they were again numerous, and it became evident that the reduced numbers observed during the winter were not due to the death of the foraminifera, nor had they been removed from the area by currents, but had become mixed with the sediments and buried to depths from which they were difficult to recover. Therefore in determining the population per unit area on the floor of the sea from samples taken within the zone of turbulence, it is necessary to consider this mixing of the foraminifera with the sub-surface sediments as well as the seasonal variation in the density of populations.

RATE OF SURVIVAL

Since the life span of *Elphidium crispum* living in tide pools is one year, the annual rate of increase is equal to the rate of mortality, and is in excess of the maximum number of individuals observed in the population at any one time.

We have said that the annual rate of productivity in this life zone is about thirtyfold, therefore the rate of survival from one period of reproduction to the next is about one in thirty. The rate of mortality for juveniles is probably high because they are used as food by myriads of small invertebrates that inhabit approximately the same ecological niche, and surf action no doubt removes large numbers from the pools, most of which fail to reach a suitable habitat. By June the size of the tests make them undesirable as food to most animal associates, and the increasing protection afforded by the growing

coralline algae, together with smoother water greatly reduces the rate of mortality during the summer and early fall. October storms which send heavy breakers crashing into the pools erode the algae so that much of the normal habitat of *E. crispum* is destroyed and with it a large portion of the foraminiferal population.

In the sublittoral zone the population near the beginning of the reproductive season on March 14, was 245 per sq. ft. compared with 1,225 per sq. ft. on June 15, which was the maximum population observed. In 1939, 10 per cent of the population, or about 25 per sq. ft., that had survived the winter failed to reproduce so that the 90 per cent which had reproduced gave rise to a population of about 1,200 individuals per sq. ft. which is equal to an average rate of productivity of 5.5 juveniles per individual that had survived till June 15, when the tests had from 16 to 24 chambers. The actual rate of reproduction was about fortyfold, therefore the rate of mortality to date was 34.5 in 40 or about 86 per cent. This rate of mortality is probably higher than that in the tide pools for the same period.

Turbulence and current action no doubt remove numbers of foraminifera from the beds to unfavorable areas where they cannot survive, while others become buried in the sediments to a depth from which they are unable to escape. The common shrimp *Crago vulgaris* which utilized foraminifera as its primary source of food throughout the winter, continued to eat the foraminifera, especially the smaller individuals, for several weeks after an abundance of other food had become available as may also have been the case with other bottom feeding organisms.

Empty tests removed from a sample of sediments taken in August were infiltrated with gelatine, hardened in formalin, and later decalcified, stained and cleared in much the same manner as that used in preparing living foraminifera for cytological study. When these gelatine casts were examined microscopically it was possible to detect the presence or absence of communicating passages which open between the proloculus and adjacent chambers in megalospheric tests during gametogenesis, thus making it possible to determine that portion of the population that had survived to reproduce from those which had terminated their existence from some other cause. From 100 tests so prepared 72 gave evidence of having been modified during reproductive activities and it would appear that 28 per cent, many of which were juveniles having

less than 20 chambers, had died from other causes. Cytological evidence suggests that not less than 3 per cent of the total died from parasitism by protozoa and nematodes, and that the remaining 25 per cent had either passed through the digestive tract of a metazoan organism or had died of starvation while buried in the sediments.

Evidence of a long term fluctuation in the population of the sublittoral zone is suggested by the difference in numbers of megalospheric individuals that had survived for more than one year in 1938 compared with 1939. On July 15, 1938, this amounted to 271 in a sample of 1,242 or 22 per cent, compared with 193 in 1,181 or somewhat less than 10 per cent on July 15, 1939 (Fig. 3). This difference resulted primarily from the failure of a larger proportion of megalospheric individuals to reproduce in the spring of 1939, which could have resulted from a failure in the food supply at a critical time since it would seem that reproduction is closely associated with a period of relative dormancy, followed by one of heavy feeding, and coincides with the spring outburst of phytoplankton production. In latitudes where there are only slight seasonal variations in ecological conditions and the food supply is relatively constant, reproduction may occur at any time after the foraminifera have approached a maximum growth stage.

RATE AT WHICH THE TESTS ARE CONTRIBUTED TO THE SEDIMENTS

The tests of *E. crispum* and its geographic subspecies are exceedingly resistant to erosion although one does occasionally find tests of which little remains other than the mass of calcium carbonate that filled the umbilical area. These eroded tests are most numerous where tidal streams cause frequent redeposition of the sediments and are seldom if ever the result of partial digestion by larger animals. Many invertebrates, including certain ecinoderms, eat enormous numbers of foraminifera, but the invertebrates which we have maintained in aquaria in order that the faecal material could be examined microscopically, had little effect upon the tests of the foraminifera which we were able to recover, and it is evident that tests of *E. crispum* or similar species pass through the digestive tract of such invertebrates as holothurians and astropectens time after time without being changed appreciably. Broken tests of both liv-

ing and dead *E. crispum* were not uncommon in the surface sediments during the winter, and it would seem that these had been crushed between the mandibles of arthropods, particularly the shrimp *Crago vulgaris*, for in the digestive tract of this species, fragments of tests were frequently found.

The empty tests of the earlier developmental stages of *E. crispum* were uncommon in regions where mature individuals were most abundant, although smaller species of foraminifera inhabit these same areas. Enormous numbers of juvenile foraminifera are eaten by bottom feeding organisms and the tests of some species may be digested, but from the absence of small worn tests of *E. crispum* in the sediments it would seem that the great majority of these were removed from the beds by currents in the same manner that clay and silt were removed. These smaller tests are deposited in quiet water where they do not constitute an important part of the sediments, although we have observed deposits consisting largely of tests of minute species and the juveniles of larger species that had been transported from other areas.

It was stated that the annual rate of mortality of *E. crispum* living in tide pools was equal to the total number of individuals produced each year, and it seems probable that the number of tests washed from the tide pools that persist to become a part of the sediments of the sublittoral zone are at least equal to the maximum populations observed during the early summer. Failure to find an appreciable number of tests of the tide pool type of *E. crispum* in the sediments of the sublittoral zone suggest the extent to which they become dispersed over the floor of Plymouth Sound.

In the sublittoral zone the number of tests annually contributed to the sediments also approximates the maximum population observed including those which had survived from the preceding year. We have said that a population of 1,225 per sq. ft. was observed in Plymouth Sound and that there is little evidence that appreciable numbers of tests of this species are destroyed by having been eaten by larger organisms or through erosion except under the conditions mentioned; therefore it would seem that in the more populous areas within Plymouth Sound the number of *E. crispum* contributed to the sediments annually was well in excess of 1,000 per sq. ft. Failure to find numbers of the larger tests of this species in the muds of adjacent areas

suggests that a considerable proportion of the tests remained where they had developed. This is borne out in part by the accumulation in the area north of Drake's Island of considerable amounts of coal particles which have about the same density as the tests of the foraminifera. This coal must have accumulated over many years, because the number of coal burning ships now entering these waters is small, or more likely it may have remained in the sediments from the time when coal burners were more numerous.

In areas in which *E. crispum* are numerous an estimate of the rate of sedimentation made from the probable rate at which tests are contributed to the sediments would have little significance because turbulence and currents at these shallow depths cause much shifting of bottom materials. However the relative uniformity of populations of foraminifera over considerable areas on the floor of the sea and the slight variation in the rate of productivity that might be expected over long periods make it seem probable that the rate of sedimentation could be estimated from the rate at which tests are contributed to the sediments compared with the number of tests in core samples from the same area.

GEOLOGICAL SIGNIFICANCE

The use of fossilized tests of foraminifera in making geological correlations, especially in Petroleum Geology, is well known, although it is not generally understood how small a part they have had in producing the carbonaceous material from which oil was probably derived. As we have said, a foraminifer terminates its existence by reproducing, or is eaten by some Metazoan organism, so that their only organic contribution to the sediments is in the small amount of animal matter to be found in the walls and lining of the test.

The distribution of *Elphidium crispum* and related species is limited to shallow coastal waters and the tests are common in sediments that were deposited along the coasts of Tertiary Seas. In California sandy lenses dating from the Miocene as those of the Lomitis quarry near San Pedro, or as determined from well cores from adjacent oil fields often contain large numbers of well preserved tests of this species together with fragments of *Balanus*, *Mytilus*, and other neritic material. When a foraminiferal assemblage from a similar formation includes species that tolerate

water of low salinity, much fresh water must have entered the region at least during the rainy season, while the presence of species found only in warm water suggest the lower limit of temperatures in the sea, and when tests of pelagic species are numerous, typically oceanic conditions probably existed near the coast, or strong currents from such a region flowed over the beds. The tests of *E. crispum* are especially resistant to erosion so where numbers of worn tests of this species are found together with an admixture of tests of smaller and less worn tide pool or reef species, the frequent reworking of the sediments by strong tidal currents is suggested, or when mixed with species that live only in deep water it is probable that the latter had been derived from an exposure of an earlier horizon. *E. crispum* and related species do not thrive where there is an excessive amount of turbulence or current action. Where sediments consist largely of mud, the occurrence of appreciable numbers of a large species of *Elphidium* over a considerable area would suggest that they had developed in a protected shallow bay or in a sea where strong winds were of infrequent occurrence, since the only place we have taken such a species on a mud bottom was in the Java Sea where winds of gale velocity are unusual.

The foraminiferal assemblage is only one of many guides available to the stratigrapher in his attempt to reconstruct the ecology of a geological horizon, although it is perhaps the most numerous and dependable one. It is only through our knowledge of assemblages found in faunal facies along traverses extending from existing shores seaward that it is possible to interpret effectively assemblages found in geological facies. The bathymetric distribution of foraminifera in coastal waters is important to the interpretation of the paleontological record and is receiving much attention at this time. When data of this nature are published they should include oceanographic data in so far as these data are available, since this information is often difficult or impossible to obtain elsewhere (see Vaughan 1940 —and Report of the National Research Council 1941).

SUMMARY

Several papers in the recent report of the subcommittee on the Ecology of Marine Organisms of the National Research Council May, 3, 1941 discuss the use of foraminifera in making stratigraphic correlations and in paleoecology, and

stress the need for further knowledge concerning the life activities of these marine rhizopods in the sea.

No previous attempt to deal with populations or the productivity of the foraminifera in the sea has come to our attention and although the present paper is limited in scope, the described methods offer a means of solving many problems that are of interest to students of marine sediments, both recent and geologic. *Elphidium crispum* was used to demonstrate the results of this work because it perhaps best exemplifies this group of Protozoa. Further the tests of this species when numerous in Tertiary formations are a guide to the probable depth and proximity to the coast at which the sediments were deposited and the life cycle has also provided the biologist with a classic example of dimorphism resulting from an alternation of generations.

When *E. crispum* is killed, hardened, decalcified, stained, and cleared it is possible to determine the number of chambers, the number and condition of the nuclei, whether the individual was about to reproduce, was feeding actively, or was in a dormant condition. Frequency distribution curves based on the number of chambers in both microspheric and megalospheric individuals in samples of populations taken at intervals of one month for twelve months show that in tide pools the life span is one year, and the life cycle including a sexual and an asexual phase two years, while in the sublittoral zone the life span is one or two years and the completion of the life cycle requires two, three, or even four years. Although the usual life span is the same in both life zones, the rate of growth in numbers of chambers was found to be about 40 per cent greater and the diameter of the test 60 per cent larger in *E. crispum* living in the sublittoral zone compared with those living in the littoral zone. A similar dualism was observed in other regions and in other species and may be related to the relative abundance of food in the two life zones.

The rate of reproduction of a foraminifer may be estimated from the number of progeny produced by microspheric agamonts in cultures and the ratio of megalospheric to microspheric individuals in the sea. In *E. crispum* the annual rate of productivity for the two generations was found to be about thirtyfold and fortyfold respectively in the littoral and sublittoral zones. The population per unit area on the floor of the sea was found to exceed 1,000 per sq. ft. in some

regions and was obtained from the number of protoplasmic casts in samples of sediments taken with a special suction grab after the sample had been treated with formalin and the tests dissolved in acidified alcohol. It was found that the tests of *E. crispum* are not destroyed in passing through the digestive tract of the invertebrates studied, and usually show slight evidence of erosion except where the sediments are shifted about by tidal streams and storm waves. Since reproduction terminates the life of the individual and both sexual and asexual reproduction is for the most part limited to a brief period in the spring, the annual productivity of the species can be easily determined.

If the number of tests contributed to the sediments annually were determined for several species living on a more stable bottom and these numbers were compared with the numbers of tests in core samples from the same area it would be possible to estimate the rate of sedimentation.

Foraminifera usually terminate their existence by reproducing or are eaten by larger organisms, and the empty tests of most species contain little organic matter. Although the use of the tests in petroleum geology is well known, it is not so generally understood how small a part they have had in the production of petroleum, however, the population of benthonic foraminifera in the sea is related to the amount of food in the water and in turn to the amount of organic matter in the sediments.

ACKNOWLEDGMENTS

This is the second of a series of papers made possible through a John Simon Guggenheim Memorial Foundation Fellowship, 1938-39, and 1939-40, and a Rhumphius Fellowship granted by the Treub Laboratories of the Netherlands East Indies, 1940-41. Much of the technical work was done by my wife, Ethel, who also assisted with the manuscript. All samples were collected personally or under personal supervision, and have been preserved for further reference.

We wish to express our appreciation to those of the staff of the Marine Biological Association at Plymouth and the Oceanographic Laboratory at Woods Hole who have helped to make the work possible, and especially we wish to acknowledge the assistance of Captain "Bill" Searles of the *Gammarus* who also helped J. J. Lister collect material at Plymouth for his monograph on the Foraminifera, 1895.

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PLATE I

Figs. 1, 4, 8 and 11, $\times 76$; Figs. 2, 3, 5, 6, 7, 9 and 10, $\times 220$

FIG. 1. Horizontal section through a fifty seven chambered megalospheric gamont showing the arrangement of the chambers and the position of the nucleus.

FIG. 2. Megalospheric nucleus showing many small endosomes and a large one that is vacuolated.

FIG. 3. Horizontal section through a thirteen chambered megalospheric juvenile in which the nucleus has remained in the proloculus.

FIG. 4. Cross section through a megalospheric gamont showing retral processes, foramina, and canals.

FIG. 5. Horizontal section through early chambers of a megalospheric gamont showing that only one other chamber communicates by a foramen with the proloculus.

FIG. 6. Similar to the above except that the several chambers surrounding the proloculus now communicate by secondary foramina with this primordial chamber.

The presence of many minute nuclei in all chambers attests that gametogenesis is well advanced.

FIG. 7. Similar to Fig. 6, except that multiple fission followed by binary fission of the resulting gametocytes has produced mononucleate gametes which occupy all chambers and the interseptal and spiral canals.

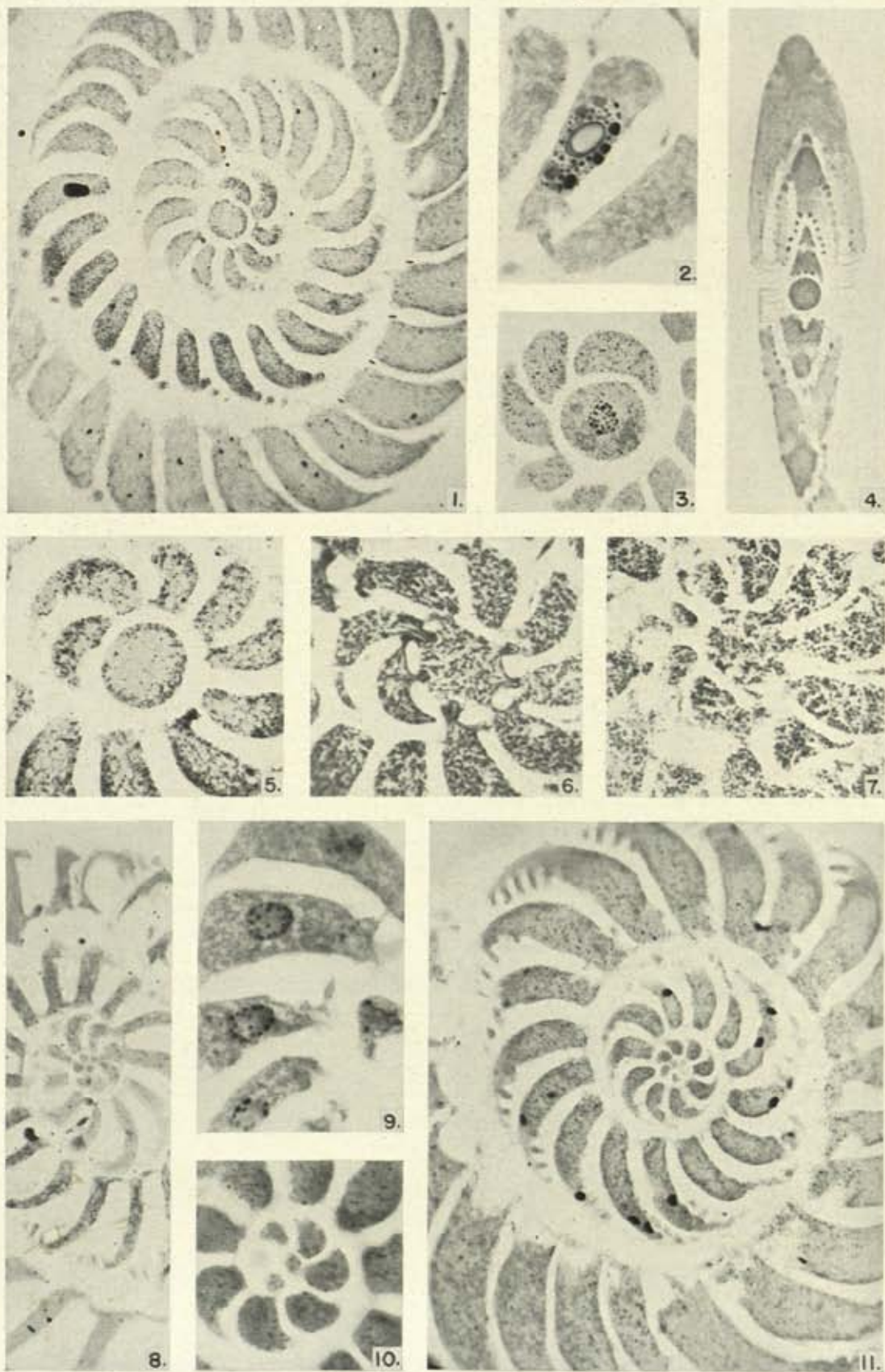
FIG. 8. Microspheric individuals showing shrinkage of the cytoplasm typical of winter dormancy. This condition was not observed at any season in warmer climates.

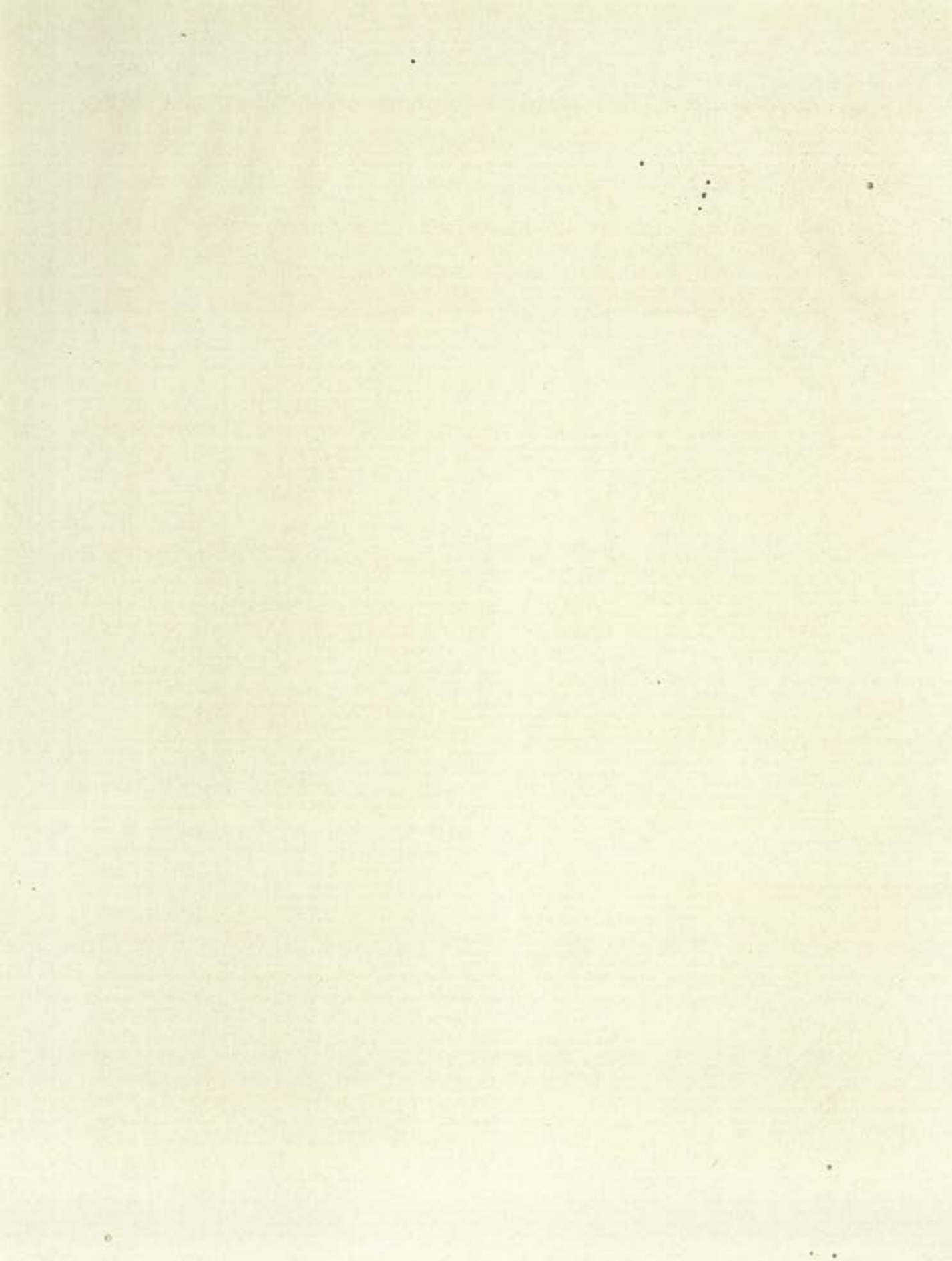
FIG. 9. Section showing four nuclei typical of vegetative microspheric agamonts.

FIG. 10. Early chambers of a microspheric agamont.

FIG. 11. Horizontal section of a microspheric agamont showing the arrangement of the chambers and the distribution of the many nuclei.

PLATE I





THE HEALTH OF REGISTRANTS AND THE PRESIDENT'S PLAN OF REHABILITATION

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(Read November 22, 1941)

SELECTIVE Service is charged with the function of procurement of men for the Army. More than 17,000,000 men have been registered to date and more than 2,000,000 have been examined and 1,000,000 men inducted into the Army.

Selective Service reveals the average registrant as 25.7 years of age, 5 feet 7½ inches tall and weighing 150 pounds. This compares favorably with the average draftee of World War I, who was also 5 feet 7½ inches tall, but who weighed only 142 pounds. The average for the soldier of the Civil War was 136 pounds, or 14 pounds less than that of the average registrants today. His average height was 5 feet 7½ inches. It appears, therefore, that the height of our young men is unchanged during the last eighty years, but that the weight is somewhat increased. This latter fact is not in keeping with the belief held by many that malnutrition is exceedingly prevalent among American citizens. It is difficult, under existing conditions, to reconcile this increase in weight with widespread want of food or serious lack of nutrition.

The average height of registrants qualified for general military service was 68.1 inches and the average weight was 152 pounds. The height of registrants examined varied from 54 inches to 88 inches, and 98.3 per cent were between 60 inches and 78 inches, which are the minimal and maximal heights, respectively, for acceptance by the Army.

Registrants varied in weight from 85 pounds to 385 pounds and 93 per cent were between 100 pounds and 190 pounds. The minimum weight for admittance into the Army for registrants 60 inches tall is 105 pounds and the standard weight for a registrant 78 inches tall is 184 pounds.

Selective Service examinations also reveal that great differences exist in the health as recorded in various parts of the country. A "Health Belt" is found in a group of western States centering around Colorado. A somewhat similar belt of good health was found during the last war. The poorest physical condition is encountered in some of the southern States. The difference in health

in some of these areas is quite marked; thus, for every 10 men examined in Colorado, 7 are found fit for service, whereas in one of the southern States, only 3 are acceptable. It must be realized, however, that these figures relate solely to the results of the examination, and do not cover the question of resistance or immunity to disease. In the last war, during epidemics of disease, it was found that men from these healthy areas were as susceptible, or even more susceptible at times, than the young men from other parts of the country.

THE RESULTS OF PHYSICAL EXAMINATION

Of the 2,000,000 young men throughout the length and breadth of the land who have undergone careful physical examination at the hands of Selective Service and the Army Induction Boards, one million have fallen short of Army requirements. One hundred thousand (100,000) have been rejected for varying degrees of illiteracy and 900,000 for physical and mental deficiencies, defects, disorders or diseases. Four hundred and thirty thousand (430,000) have been classified IV-F as unfitted for any form of military service, and 470,000 as fit only for limited service. Thus 50 per cent of the registrants to date have fallen short of the standard requirements for service with the military forces.

These figures are not to be interpreted as representing 50 per cent invalidism of the registrants examined, or as indicative of 50 per cent illness of the population in general. They simply represent unfitness for military service according to the standard requirements that have been set up by the Army.

Apparently, Selective Service has uncovered a vast field of physical unfitness. The registrants concerned, in the majority of instances, are not ill; they are not sick; they are at work and carrying on satisfactorily despite their defects and deficiencies. They suffer from hidden potential sources of disease and cover up as they carry on. Defects from which they suffer today, minor as they may be, may prove responsible for serious

illness in the years to come. If these defects are serious enough to render the individual unfit for military service, they undoubtedly are playing at least some role in the efficiency of the individual's carrying on his ordinary occupations in civilian life.

To some, the state of physical unfitness appears a matter of minor importance. To the Army, it is a matter of major significance since it is cutting down manpower for military service to the extent of at least 50 per cent. To the nation, this unfitness comes as a decided shock. It constitutes a national weakness heretofore not properly appreciated and calls for immediate correction from the standpoint of securing manpower for the Army, and constitutes a challenge to the nation for the program of building up of physical fitness.

When we come to a breakdown of the various causes for rejection, we find them listed as follows (Table 1):

TABLE 1
THE PHYSICAL REJECTIONS OF REGISTRANTS

Cause	Number of Cases	Percentage
Dental defects	188,000	20.9
Defective eyes	123,000	13.7
Cardiovascular diseases	96,000	10.6
Musculo-skeletal defects	61,000	6.8
Venereal diseases	57,000	6.3
Mental and nervous diseases	57,000	6.3
Hernia	56,000	6.2
Defects of ears	41,000	4.6
Defects of feet	36,000	4.0
Defective lungs, including tuberculosis	26,000	2.9
Miscellaneous	159,000	17.7
	900,000	100

INCIDENCE OF DEFECTS

The major pathology indicates the reasons why registrants were rejected, but does not afford an accurate index as to the incidence and prevalence of diseases and defects among them. In this study a maximum of three defects was recorded. A total of 27,031 defects were tabulated from the 19,923 reports of physical examination, an average of 1.4 defects per registrant examined. No defects were recorded, however, for 5,741 registrants, or 29 per cent of the total number examined. Of the total of 27,031 defects one or more was recorded for each of 14,182 registrants, an average of 1.9 defects per registrant with defects. Two defects were recorded for each of

8,433 registrants and three defects for 4,416 registrants.

In Table 2 there is a list of the defects or diseases tabulated by broad classifications with the rate per thousand registrants examined.

TABLE 2
INCIDENCE OF DEFECTS FOUND IN 19,923 REGISTRANTS
EXAMINED BY SELECTIVE SERVICE LOCAL BOARDS

Defect or Disease	Defects Found	Defects Per 1,000
Eyes	2,305	115.7
Ears	887	44.5
Teeth	2,795	140.3
Mouth and gums	1,273	63.9
Nose	1,372	68.9
Throat	1,321	66.3
Lungs	327	16.4
Tuberculosis	114	5.7
Cardiovascular system	2,000	100.4
Blood and blood-forming organs	19	1.0
Hernia	1,287	64.6
Kidneys and urinary system	279	14.0
Abdominal viscera	244	12.2
Genitalia	1,175	59.0
Venereal	695	34.0
Skin	2,308	115.8
Hemorrhoids and rectal defects	610	30.6
Varicose veins	531	26.7
Mental and educational deficiency and illiteracy	239	12.0
Mental disorders	362	18.2
Neurological	454	22.8
Musculo-skeletal	2,018	101.3
Feet	2,888	145.0
Endocrine disturbances	319	16.0
Tumors	228	11.3
Infectious, parasitic and epidemic diseases	7	0.4
Other diseases and defects	974	48.9
Total	27,031	1,356.8

This tabulation includes defects which do not disqualify as well as defects which do disqualify for general military service. Defective feet accounted for the largest number of diseases and defects recorded for any single organ, section or system of the body and comprised 10.7 per cent of the total number of defects tabulated. Dental defects, which was the largest cause of rejection for military service, comprised 10.3 per cent of the diseases and defects. In addition to non-disqualifying defects, a large proportion of the disqualifying defects are minor insofar as health conditions are concerned. Many defects are a cause for rejection for service in the Army, but in no way hinder the performance of many civilian occupations.

EFFECT OF AGE ON SELECTION AND REJECTION

Inasmuch as the reports of physical examination considered in this survey were for men examined prior to May 31, 1941, registrants between the ages of 21 and 36 were included as well as a small number of men between the ages of 18 and 21 who volunteered through the Selective Service System for military service. Two-thirds of the registrants examined by local boards were between the ages of 21 and 28. Registrants between the ages of 28 and 36, inclusive, accounted for 31.3 per cent of the total number examined, and the volunteers between the ages of 18 and 21 accounted for 2.1 per cent of the total registrants examined.

The rate of rejection of registrants between the ages of 31 and 36 was nearly twice as great as that between the ages of 21 and 25, inclusive. Sixty-one per cent of the registrants between the ages of 31 and 36 were unacceptable for general military service as compared to 45 per cent between the ages of 26 and 30, and 34 per cent between the ages of 21 and 25. The percentage who were qualified for general military service varied from 70.5 per cent for registrants 21 years old to 29.9 per cent for registrants 36 years old at the time of physical examination. The rela-

tionship that exists between the registrants' age and availability for general military service is shown in Table 3 and Chart II.

TABLE 3
AGE OF REGISTRANTS BY AVAILABILITY
FOR MILITARY SERVICE

Age ¹	Num- Exam- ined	Percent- age of Total Exam- ined	Qualified for General Military Service		Qualified for Limited Military Service		Disqualified for Military Service	
	Num- ber	Per Cent	Num- ber	Per Cent	Num- ber	Per Cent	Num- ber	Per Cent
18	153	0.8	129	84.3	8	5.2	16	10.5
19	143	0.7	118	82.5	13	9.1	12	8.4
20	127	0.6	94	74.0	17	13.4	16	12.6
21	2,083	10.4	1,469	70.5	347	16.7	267	12.8
22	2,688	13.5	1,810	67.3	511	19.0	367	13.7
23	2,248	11.3	1,504	66.9	393	17.5	351	15.6
24	1,372	6.9	1,222	89.1	343	24.9	307	22.3
25	1,692	8.5	1,034	61.1	331	19.6	327	19.3
26	1,492	7.5	905	60.7	276	18.5	311	20.8
27	1,189	6.0	682	57.4	268	22.5	239	20.1
28	1,071	5.4	576	53.8	260	24.3	235	21.9
29	839	4.2	435	51.8	213	25.4	191	22.8
30	869	4.4	400	46.0	226	26.0	243	28.0
31	697	3.5	306	43.9	188	27.0	203	29.1
32	681	3.4	282	41.4	188	27.6	211	31.0
33	669	3.4	282	42.4	188	28.1	199	29.7
34	602	3.0	212	35.2	159	26.4	231	38.4
35	527	2.6	176	33.4	172	32.6	179	34.0
36	157	0.8	47	29.9	54	34.4	56	35.7
Unknown	124	0.6	71	57.2	29	23.4	24	19.4
Total	19,923	100.0	11,754	59.0	4,184	21.0	3,985	20.0

¹ Age at last birthday at time of physical examination

ESTIMATED NUMBER OF SELECTEES REJECTED

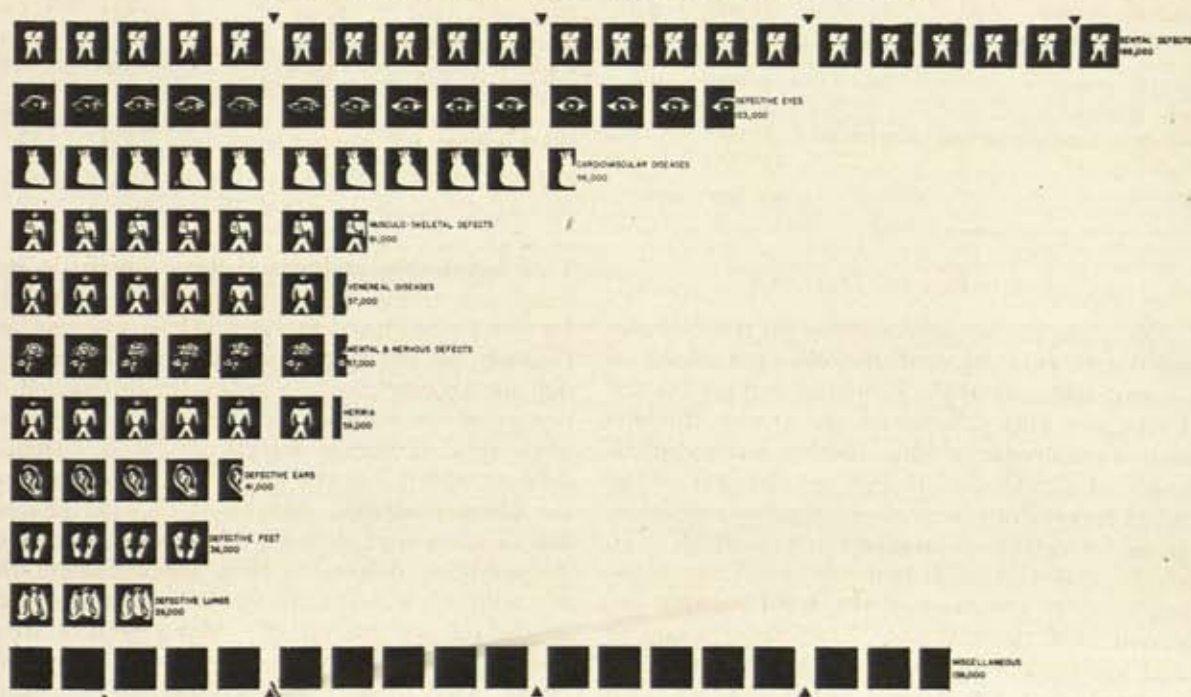


CHART I. Each symbol represents one per cent of the 900,000 rejected.

CLASSIFICATION FOR MILITARY SERVICE IN RELATION TO AGE

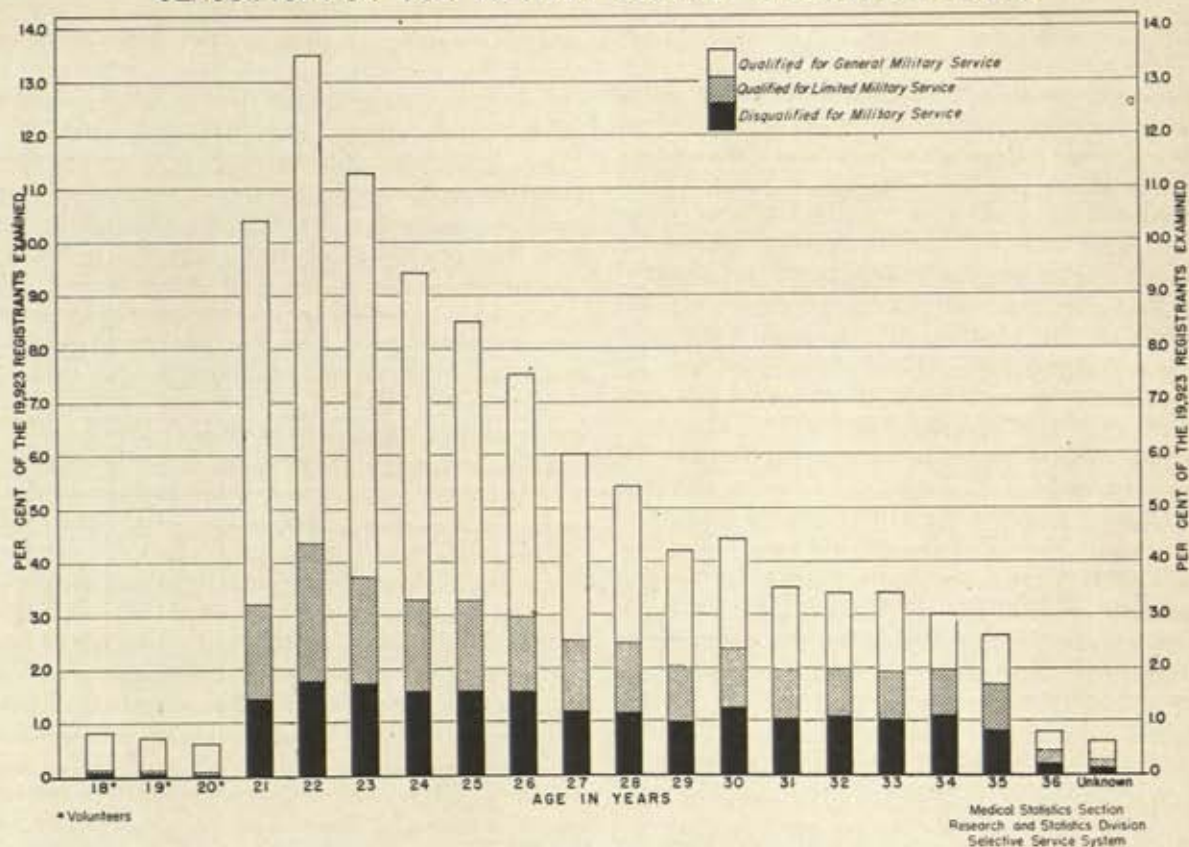


CHART II

OCCUPATION

About one-seventh of all registrants examined were unemployed at the time of examination. The largest group of employed registrants physically examined were operatives and kindred workers comprising about 20 per cent. Most numerous among operatives and kindred workers were chauffeurs, truck drivers, delivery-men, weavers, knitters, spinners, assemblers, and operators of lathes, drill presses and other machines. Farmers and farm laborers, the second largest employed group, accounted for 14 per cent of the total number examined. Craftsmen and foremen, which accounted for 8 per cent of all registrants examined, were mostly carpenters, cabinet makers, pattern makers, mechanics, repairmen, machinists, millwrights, tool makers, painters, paper hangers and printers. Approximately one per cent of the registrants examined were students. The occupations of the registrants examined are shown by broad classifications in Table 4.

TABLE 4
OCCUPATIONS OF 19,923 REGISTRANTS
PHYSICALLY EXAMINED

Occupation	Number of Registrants Physically Examined	Percentage of Total Examined
Professional workers	590	3.0
Semiprofessional workers	226	1.1
Farmers (owners, tenants and crop- pers) and farm managers	1,099	5.5
Proprietors, managers, and officials ex- cept farm	779	3.9
Clerical and kindred workers	1,548	7.8
Salesmen	878	4.4
Craftsmen, foremen and kindred workers	1,679	8.4
Operatives and kindred workers	4,064	20.4
Domestic service workers	56	0.3
Protective service workers	64	0.3
Service workers, except domestic and protective	936	4.7
Farm laborers and foremen	1,683	8.4
Laborers, except farm and mine	2,487	12.5
Nonclassifiable returns	571	2.9
Emergency workers and unemployed ..	3,042	15.3
Students	221	1.1
Total	19,923	100.0

RACE, URBAN-RURAL RESIDENCE, AND PLACE OF BIRTH

The ratio of Negro registrants to the total number examined was approximately the same as the ratio of Negroes to the total population, 11 per cent. Registrants of other races, which accounted for less than one per cent of the total number examined, were mostly Chinese, Japanese and Indians. The rate of rejection for Negro registrants was 42.6 per cent as compared to 40.8 per cent for white registrants. Two-thirds of the registrants examined were from urban communities. The rate of rejection for registrants from urban areas was 42.4 per cent as compared to 38.1 per cent for rural areas.

The United States and its territories was the place of birth of 97.3 per cent of the registrants examined, most of the others having been born in Canada, British Isles and Europe. The rate of rejections for native born registrants was 40.9 per cent as compared to 45.6 per cent for registrants born outside the United States and its territories. This, perhaps, can be accounted for by the differences in age groups.

REHABILITATION OF REGISTRANTS

Because of the relatively poor physical state of 50 per cent of the registrants examined and because of the urgent need of manpower for the military forces, the President called a conference at the White House on October 9, of this year to determine what measures should be instituted for the correction of this situation.

The President's Plan for Rehabilitation provided for the correction of remediable defects of 200,000 registrants, the program to be carried out by Selective Service through its existing boards and personnel, and to be effected in the registrant's home town under the supervision of Selective Service in conjunction with the family doctor and dentist, and County Medical and Dental Societies, the professional work to be done at a reasonable cost for which funds are to be made available.

The rehabilitation of 200,000 men represents a large order. Success demands the best services and the closest coöperation of the doctors and dentists and the clinics and hospitals throughout the entire country, the project calling for the maximum efficiency of the two professions concerned. Rehabilitation should be effected with the minimum risk to the registrants. Hence, Selective Service has adopted "safety first" as its

rehabilitation slogan. Such a program calls for careful planning, wise selection of candidates and skillful handling of them in the application of remediable measures.

For Army purposes, all defects cannot be regarded alike relative to satisfactory rehabilitation. The Army, through long years of experience, has determined what diseases and disorders readily lend themselves to successful rehabilitation that produces "fit men" who can stand up satisfactorily under the rigorous demands of Army training and service. Hence, the Surgeon General of the Army, James C. Magee, has been consulted freely as to preference in the types of defects to be remedied. But for conservation of effort and expense, still more is required. It is necessary to know in advance, before rehabilitation is actually attempted, which individual registrant will be acceptable to the Army when the remedial measures have been applied. Hence, arrangements have been perfected whereby Army examination given prior to rehabilitation will determine and certify, so to speak, subsequent acceptance of the individual after his rehabilitation has been completed. This Plan aims to facilitate the President's objective quickly to rehabilitate a large number of suitable registrants who will be immediately inducted into the military forces, thereby actually increasing the manpower of the country.

Since dental defects are responsible for the greatest number of rejections in America, and since they lend themselves readily to remedy and because the risk of remedy is exceedingly remote, it is planned to rehabilitate 100,000 victims of dental disorders.

Among the medical deficiencies and defects, the following groups will lend themselves readily to rehabilitation: deficiency in vision, which has not been adequately corrected; certain cases suffering from conjunctivitis, pterygium, or from scars of deformities of the lids; among cardiovascular diseases, many may be salvaged who are found to present borderline hypertension, mild tachycardia, functional murmurs, extra systoles, low blood pressure; among musculo-skeletal defects, many should be reclassified, especially those who complained of aches and pains of various kinds at time of examination, who, in the interim have not found it necessary to be under the care of a qualified physician; likewise, many cases of first degree flat feet can be salvaged.

A large number of individuals who were found suffering from venereal diseases, particularly un-

complicated gonorrhea, may, by this time, have recovered, and reclassification may find them acceptable for induction.

Among the miscellaneous group, there are undoubtedly a very considerable number of disorders contributing little to morbidity or mortality, yet easily susceptible to correction. In this category are many suffering from underweight, overweight, from tonsillitis, nasopharyngitis, nasal polypi, deviation of the septum. Many others suffering from moderate degrees of skin diseases, acne or furunculosis and others with external hemorrhoids or presenting evidence of postural or orthostatic albuminuria, transient glycosuria, phimoses, etc.

Another group of diseases is quite unfavorable from the standpoint of rehabilitation. This group includes the victims of nervous and mental disorders, uncorrectable defects of vision or hearing and patients who have suffered chronic diseases of the lungs, especially tuberculosis and victims of syphilis. From these groups, it will be impossible to find many who can be rehabilitated to meet the requirements of the military forces.

For the present at least, a conservative position is being taken towards patients suffering from conditions requiring surgical interference, such as hernia, varicocele, etc. Army experience has established the fact that more is needed in many of these cases than the mechanical cure. Surgical risk attends all forms of major operation, and to a slight extent, even minor surgical measures. Surgery should not be employed in this program except on request of the registrant and, for reasons which are obvious, with the assumption by him of full responsibility for the surgical risk. The thought must also be given to possible development of untoward psychical reactions which may prove detrimental to satisfactory Army service. Selective Service is therefore giving very careful consideration to the different types of rehabilitation in order that the greatest benefit may accrue to all persons interested, the registrant, the Army and the national health in general.

PREHABILITATION

Rehabilitation takes cognizance of defects at the time of examination by Selective Service or at the Army examining station. There is, however, another procedure whereby these defects can be discovered and corrected in advance of the official examination. For this plan, Selective Service has suggested the term Prehabilitation.

Prehabilitation provides that: (1) through education of the registrants, the standard requirements of the Army are made known; (2) that registrants falling short of these requirements consult their family doctor and dentist; (3) have their remediable defects corrected; (4) be given a certificate to this effect to present to their examining boards. The plan of Prehabilitation has already been published covering some five articles that have appeared in the *Journal of the American Medical Association*, *Journal of the American Dental Association* and other Journals.

In many respects, Prehabilitation is a form of preventive medicine, especially the correction of minor defects before they develop into serious etiological factors such as might be concerned in the pathogenesis of more serious types of disease. Prehabilitation has been employed in the University of Minnesota to render male students of military age fit for examination and for service.

CONCLUSION

The facts revealed by Selective Service relative to the widespread prevalence of defects, deficiencies, disorders and diseases among registrants should exert a salutary effect on the Nation as a whole. Once their nature, prevalence, distribution and their menace to health and efficiency are disclosed, they are more apt to receive appropriate attention and thereby be eradicated. There is no doubt that the correction of these defects as they develop would contribute largely to the elevation of public health onto a higher plane. *Better Public Health can be attained only through Better Individual Health. Better Individual Health can be attained only by the prevention of disease and the correction of minor defects as they arise.*

THE MYSTERY OF COR CAROLI

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ABSTRACT

Cor Caroli, or α^2 Canum Venaticorum, has a spectrum of type A, with fairly strong lines of *H*, *Mg* II, *Fe* II, *Cr* II and with a temperature of about 10,000°. Its spectral absorption lines show unusual changes in intensity, and until recently the star was believed to be unique in this respect. Several other A-type stars are now known which show similar changes. The spectral lines of α^2 Can Ven are arranged in three groups (the designations of which must not be confused with the designations of spectral type or temperature). Group A consists of *Eu* II, *Gd* II, *Dy* II and other rare earths, *Fe* I, *Ti* II, etc. The lines of *Eu* II show a variation in equivalent width by a factor of at least 10; the other elements, especially *Ti* II, *Fe* I, *Ce* II, *Sa* II, show smaller ranges. The period is constant, $P = 5.46939$ days. Group B consists of several elements, such as *H*, *Si* II, *Fe* II, and *Cr* II, which vary in the opposite sense of group A lines. The range is greatest for *Cr* II. Group C consists of lines which remain constant in intensity. Examples are *Mg* II and *Sr* II.

The lines of groups B and C are essentially constant in velocity. The strong lines of *Eu* II show large negative displacements from about 1.6 days prior to their intensity maximum, and large positive displacement until about 1.5 days after intensity maximum. During the remaining 2.4 days the lines are so weak that blends may interfere with the measurements. The lines of all groups probably originate in the star, but not necessarily in the same atmospheric layer.

The great strength of the rare earths, especially *Eu* II, at certain phases is very strange. The variation in intensity cannot be explained in terms of Saha's theory of thermal ionization, because *Sr* II, the ionization potential of which is only 0.2 volt lower than that of *Eu* II, shows no appreciable change in intensity.

The phenomena strongly suggest that departures from thermodynamic equilibrium are operating in such a way as to produce a variable amount of suppression of double ionization near 11.2 volts, without appreciable change at 11.0 volts (*Sr* II) and with a permanent enhancement of ionization at 11.8 volts (*Ca* II). The nature of this phenomenon is not clear, but it is correlated with the variable velocities of the *Eu* II lines, and may involve a conversion of the energy of ionization into kinetic energy of motion. It is significant that the continuous spectrum of an A-type star is greatly distorted from that of a black body by the Lyman lines and the Lyman continuum. It is from the region between L_α and L_β that the ionization energy of the rare earths is derived, while the region of L_β contributes especially to the ionization of *Ca* II. A strong emission line at L_β would perhaps explain the excessive ionization of *Ca* II.

It was reported by Sir Charles Scarborough, court physician of King Charles II, that the star now known as α Canum Venaticorum had shone

with unusual brilliance on the night of the King's return to London on May 29, 1660. In order to commemorate the event, which appeared to give divine sanction to the restoration of the Stuart dynasty in England, the Astronomer Royal, Edmond Halley, in 1725 designated this star as the center of a small constellation, the Heart of Charles, and since that time the star itself has often been called Cor Caroli.¹ The story of the brightening of α Can Ven has never been verified. It was not regarded as a suspected variable in the catalogues of Gore and of Zinner, although more recently it has been found to have a periodic variation of very small amplitude.

Our present interest in Cor Caroli depends upon the fact that it is the typical representative of a mysterious class of stars having variable absorption lines in their spectra. We know very little about these stars. Half a dozen, or so, have been discovered, mostly by W. W. Morgan at the Yerkes Observatory. But the periods are known for only two or three, and the character of the variation, or its causes, remain to this day an unsolved puzzle.

α Can Ven is a visual double star. The distance of almost 20'' between the 2.9 mag. primary (designated as α^2) and the 5.7 mag. secondary (designated as α^1) has remained constant since 1830. So has also its position angle of 228°. Both components are usually listed as spectroscopic binaries. The fainter shows a rather normal spectrum of type F. Harper found a range in the radial velocity of 17 km/sec and I have obtained similar results from spectrograms taken at the Yerkes Observatory. So far as I know no orbit of this star has been published. Incidentally, the wide separation makes it possible to guide with the slit-spectrograph on each component without any danger of contaminating the plate with the light of the other.

The bright component was originally announced as a spectroscopic binary by Belopolsky. But in the last catalogue of spectroscopic binaries from the Lick Observatory, J. H. Moore lists it

¹ R. H. Allen, *Star Names and their Meanings*, New York, 1899. I am grateful to Mr. Herbert W. Cornell of Milwaukee for this reference.

among "stars having variable radial velocity, but which are not binaries."²

The proper motion of the system is 0".233 in position angle 282°. The parallax is 0".024 and the mean radial velocity is - 3.5 km/sec.

The spectrum was first definitely classed as peculiar in 1897 by Miss Maury.³ She called attention to the weakness of *Ca* K and the great strength of *Si* II 4128, 4131 in this star of type A (according to our present Draper classification). She adds: "Some of the fainter lines appear to be peculiar in wave length, while others differ in intensity from the corresponding lines of the stars in division *a* (of her group VIII). In the weakness of the line K alluded to, this star resembles those of composite type, and its peculiarities may perhaps be due to its known duplicity. If, however, in the companion star the line K is so faint, it is difficult to explain the absence of the Orion lines."

We now know that neither the distant companion (which does not affect the spectrum in a slit instrument), nor any hypothetical spectroscopic companion of the star α^2 can produce the observed effect. The phenomenon is one frequently observed among A-type stars, as has been shown by Morgan.⁴

The peculiarities noted by Miss Maury were confirmed in 1906 by Lockyer and Baxandall. They also found that "the more pronounced lines of iron, titanium, and chromium are present, but weak," while *Mg* 4481 is strong. "The ordinary metallic arc lines, which occur prominently in the lower type stars, are lacking. Some of the strange lines, that is, lines not in the normal spectrum of the same general type, appear to be identical with those in θ Aurigae. Thus there are lines of which the wave lengths are approximately 3954.3, 4076.5, 4136.3, 4192.0, and 4376.8. . . . There are no lines of considerable intensity peculiar to α Can Ven, though some of the fainter lines seem to be peculiar to this spectrum."⁵

Incidentally, even now, we know little about the lines of Lockyer and Baxandall:

L.-B.	Int.	Modern Identification
3954.3	2	Unknown
4076.5	6	Mostly unknown, <i>Si</i> II 6.78(1); <i>Fe</i> II 7.16(3)
4136.3	2	Unknown
4192.0	3+2	Blend of <i>Si</i> II and <i>Ce</i> II
4376.8	3+1	Blend of <i>Sm</i> II and <i>Ce</i> II

² *Lick Obs. Bull.* No. 483, 1936.

³ *Harvard Annals*, 28, 96, Remark 69, 1897.

⁴ *Pub. Yerkes Obs.*, 7, Pt. 3, 1935, see especially Plate I.

⁵ *Proc. Royal Soc. London*, A77, 550, 1906.

This shows how little progress has been made in this field in the past 36 years!

The star became of particular interest to astronomers in the latter part of 1906, when Ludendorff⁶ announced that the lines of α^2 Can Ven vary in intensity. He wrote "A comparison of the best plates proved with a fair degree of certainty that the intensities of a number of lines are really variable." He mentions especially the following lines:

Ludendorff	Modern Evidence
<i>Cr</i> 4341.93 on some plates strong, on others not visible	<i>Fe</i> II 4351.76 of group B or C, but always easily visible
<i>Fe</i> 4472.88 sometimes strong, at other times absent	<i>Fe</i> II 4472.92, group C
<i>Fe</i> 4238.97 sometimes strong, at other times absent	<i>Fe</i> I 4238.82, group C, always visible
<i>Mg</i> 4481 sometimes sharp, at other times less so	<i>Mg</i> II 4481, group B, but always very strong

In view of the remarkable results obtained by Belopolsky and all later observers it is surprising, to say the least, that Ludendorff picked out precisely those lines which vary little. He either did not notice those lines which show enormous changes in intensity, or they were not in the spectrum at the time of his observations. It should be remembered, however, that the most conspicuous lines of variable intensity, namely $\lambda\lambda$ 4129, 4205 were probably beyond the range of his instrument. Ludendorff found no regularity in the variation. It must be admitted that the discovery of a star with variable lines was a remarkable result, especially in 1906, when hardly any other star of similar character was known. Ludendorff's work represents the first step in a long series of papers which were devoted to α^2 Can Ven.

The first, and perhaps most significant, of these investigations is one by A. A. Belopolsky at Pulkovo.⁷ He discovered the important group of variable lines now attributed to "group A," among which are $\lambda\lambda$ 3984, 4038, 4130, 4291, 4386, etc. From the intensities of λ 4130 he derived the period

$$P = 5.50 \text{ days.}$$

He also found a second group of lines, now designated as "group B," which vary in the opposite sense as do the lines of group A and, finally, established that several lines do not vary at all

⁶ *A.N.*, 173, 4, 1906.

⁷ *A.N.*, 196, 1, 1913.

or vary but little. Among the latter ("group C") he included *H*, *Mg*, *Ca* and *Fe*. We must be careful not to confuse the designations of the groups A and B with the names of the spectral types of the stars. α Can Ven is an A-type star and it has lines of three groups: A, B and C.

From the group A line λ 4205 Belopolsky derived a velocity curve with a considerable range, but the lines of group C and many of group B showed no conspicuous changes in velocity. Line λ 4130 agreed with λ 4205 when the former was visible, but at times of minimum intensity it disappeared completely; λ 4205 was always visible, but occasionally became very weak and sometimes double; when that happened only one component was believed to belong to the star proper.

Belopolsky concluded: "It is difficult to decide wherein to seek the cause of this phenomenon. An obvious hypothesis suggests itself, namely, that the central body is surrounded by a gaseous satellite or a gaseous ring having a condensation of matter at one point. This hypothesis is supported by the sign of the variable velocities (negative velocities preceding maximum of intensity of λ 4130 and positive velocities following maximum), but the details of the observations still present difficulties which may perhaps be cleared up after more material has been accumulated."

Belopolsky's work⁸ was very diligently continued by his pupils at Poulkovo, especially by Rossovskaya, Gerasimovič and Markov.⁹ These investigations greatly added to our knowledge of the variable lines, but gave no new concepts and no further tests of the hypothesis. Belopolsky himself attempted in 1915 to measure the line λ 4205 as a double and to derive an orbit for two visible components. But λ 4130 does not show the doubling and Coudé plates of high dispersion now rule out the double velocities. Yet, one aspect of Belopolsky's curves is of importance. He places the minimum velocity of the stronger component about 1.2 days earlier than the maximum of intensity of λ 4130. The curve is thus very unsymmetrical.

Almost immediately after the first paper by Belopolsky had appeared, Baxandall¹⁰ pointed out that five of Belopolsky's variable lines of group A are due to europium. The surprising fact that this rare-earth element should be conspicuous in an A-type spectrum was commented

upon by various speakers at the meeting of the Royal Astronomical Society at which Baxandall's paper was presented. A. Fowler suggested that¹¹ "slight disturbances in the star might bring about small changes of level sufficient to put the europium in or out of the absorbing region, and so determine the presence or absence of the lines."

Belopolsky's brilliant discovery aroused a great amount of admiration, as well as of speculation. It was thought by Stratton¹² not only "to round off Belopolsky's discovery of the binary nature of the Cepheid variables by finding one double whose components have different and visible spectra" (namely, groups A and B of the variable lines), but that the lines which neither shift nor vary present "the problem of Hartmann's fixed calcium lines all over again, complicated by the presence of several elements." Hydrogen, silicon, iron and magnesium were thought by Stratton to belong to "an envelope surrounding and moving with the system . . . (of) both components of the binary."

The next significant spectroscopic study of α Can Ven was that by C. C. Kiess at the Observatory of the University of Michigan.¹³ The star was placed upon the observing program immediately after Belopolsky's announcement in 1913 and a large number of plates were measured by Kiess for radial velocity and for the identification of lines. His table of wave lengths gave the first complete study of this interesting spectrum and served as the starting point of most later studies. The velocity curve shows the same general trend as the one of Belopolsky, but only one component was measured. Kiess stated that "maximum positive displacement occurs when the line is of minimum intensity; and maximum negative displacement when it is of maximum intensity." This is contrary to Belopolsky, who found a lag of 1.2 days between the two epochs. However, Kiess' paper does not contain a study of the line intensities, and the question arises whether he determined the epoch of maximum intensity with any precision. Fortunately for us, Miss G. Farnsworth was permitted some years ago to examine the Michigan spectrograms. With the help of this material and the published data from all other observatories she found that all epochs could be repre-

⁸ *Bull. de Poulkovo*, No. 70, 1915.

⁹ *A.p.J.*, 72, 301, 1930.

¹⁰ *Observatory*, 36, 440, 1913.

¹¹ *Ibid.*, 461.

¹² *Ibid.*, 432.

¹³ *Pub. Obs. U. of Michigan*, 3, 106, 1919.

sented by the formula

$$\begin{aligned} \text{Maximum of } Eu \text{ II} \\ = \text{JD } 2419869.720 + 5.46939E. \end{aligned}$$

The departures of 10 epochs between 1913 and 1932 are irregular and never exceed 0.1 day. This must be regarded as exceedingly satisfactory. Incidentally, all recent observations, including those at McDonald and at Mount Wilson, in 1941, are perfectly well represented by her formula. This disposes of a doubt recently expressed by Tai¹⁴ who thought that for his observations of 1938–39 maximum line-strength occurred about 1.2 days later than predicted from Miss Farnsworth's formula. I cannot explain the discrepancy, but when I apply the formula to the dates given his Table I, I find values which, with the exception of the first, are exactly one day smaller than the ones printed. This suffices to bring his observations into accord with the other series.

Returning to the paper by Kiess, we notice that he observed minimum velocity of λ 4205 on June 14.7, 1913 = JD 2419933.7. This is exactly 64.0 days later than the epoch of Miss Farnsworth's formula. Twelve times $P = 5^d 46939$ is 65.6 days. Hence maximum intensity for *Eu* II occurred 1.6 days later than minimum velocity—in excellent agreement with Belopolsky.

Kiess gave many new identifications of lines and suggested the presence of *Gd*, *Dy*, *Y*, *La* and, especially, *Tb*. The former two were confirmed by Morgan and later by Tai; *La* is uncertain according to the latter who found only some 19 unconvincing coincidences among 41 strong lines of Miss Moore's table; *Y* is definitely present. But *Tb* is uncertain, again according to Tai and also to Morgan, who examined the proposed identifications carefully and found that almost all lines formerly attributed to *Tb* were explained by *Fe* II, *Ti* II, *Cr* II, etc. This, incidentally, removes an important conclusion by Kiess. He had thought that the *Tb* lines belong to group B.

Kiess favored the idea of Fowler: "granting that there is a periodic change in level of the vapors of europium and terbium, radial motions and pressure effects combined may account for the velocity shifts observed."

Without going into further details, we may mention that the Russian investigators concluded in 1927 that the variations in line intensities were similar to those of the Cepheids. Miss Anger¹⁵

gave new curves of intensities, and concluded, in agreement with Belopolsky,¹⁶ that the spectrum has many emission lines, also of variable intensity. It is extremely difficult to decide whether these lines are real. Belopolsky thought that there were absorption lines with bright edges and also isolated bright lines. Miss Anger gave a long list of the latter, but no identifications. There are no identifications in the paper by Belopolsky. Although I have also occasionally suspected faint emission line on a few plates, I now believe that they are only spaces between absorption lines. It is, however, entirely possible that the spectrum has changed since 1928 when Belopolsky thought that the emission lines were strong.

We next come to a study by Miss Goldena Farnsworth¹⁷ of Yerkes single-prism plates on Process emulsion taken in 1931 by several observers. Miss Farnsworth measured a number of lines for radial velocity and estimated their intensities. Her velocity curve for λ 4205 agrees with that of Kiess, and minimum velocity again precedes maximum intensity by about one day. But she suspected that the "large displacement of λ 4205 at minimum (intensity) phase was due to a blend" and suggested that the blending was with *Mn* II 4205.41. The line at λ 4205.48 is now believed to be due to *Fe* II. On Coudé plates this line is clearly resolved from the *Eu* II line, but with small dispersion the blend may easily be measured when *Eu* II is very weak. She also found a number of other lines in which blends of variable components unquestionably produce spurious shifts in velocity. We shall return to this question later.

It is now appropriate to make an excursion into the field of photometry. In 1914 Guthnick and Prager found photoelectrically that α Can Ven is a continuous variable with an amplitude of 0.051 mag. The curve is roughly symmetrical. Maximum light occurred on 2420242.2 GMT, which is within 0.56 day of maximum *Eu* II intensity. All other reliable series of magnitudes by Guthnick and his associates, and most recently by Tai, agree in placing maximum light in coincidence with maximum *Eu* II intensity. But Tai, as well as the Babelsberg observers found that the range is not constant. Tai found 0.03 mag. Miss Güssow¹⁸ records variations in shape and amplitude and a shift of - 1 day in

¹⁴ *M.N.*, 100, 94, 1939; *Observatory*, 63, 134, 1940.

¹⁵ *Ap.J.*, 70, 114, 1929.

¹⁶ *A.N.*, 234, 5, 1928.

¹⁷ *Ap.J.*, 75, 364, 1932.

¹⁸ *A.N.*, 237, 334, 1930.

1928 and 1929 from the epoch of Guthnick. Sometimes the range is so small that the variation is not detectable. At other times it is fairly conspicuous. The period seems to be constant and agrees with that determined spectroscopically.

So far as I know, only C. T. Elvey has observed this star photometrically in the United States. He found variations in accordance with those of other observers. The results were never published. Tai's results were obtained in collaboration with H. E. Green at the photoelectric photometer of the 12-inch Sheepshanks refractor in Cambridge, England. The comparison star was δ UMa.

The color temperature was observed by D. R. Barber photographically at Sidmouth and the plates (14 in number) were measured by Tai. The results are regarded as somewhat uncertain because Hunter¹⁹ had failed to find a variation within the period of 5.5 days in his work at Greenwich. If the curve is real it indicates a maximum temperature of 25,000° (or B5) near light minimum and a minimum of 18,000° (A0) near light maximum. Tai remarks, however, that the *He* I lines are always absent, and that the high temperatures are probably not real.

The latest spectroscopic studies are those by Morgan²⁰ and Tai.²¹ Both contain excellent lists of lines and very full information concerning the identifications. Morgan's list is more complete, but Tai was able to use more recent laboratory data. He suggested, with a question mark, that *Ce* II might be present. The ultraviolet region was measured by me on Cassegrain plates taken at the McDonald Observatory,²² but the phase of the plates corresponded to minimum strength of *Eu* II.

We now turn to the consideration of new data secured at the McDonald Observatory in 1941. The plates were obtained by Dr. P. Swings and by me with the Coudé spectrograph on seven successive nights, from January 21 to 27, 1941. They cover the region λ 3900 to λ 4700 and the dispersion is around 2 Å/mm at the violet end and 4 Å/mm at the red. The emulsion used was Eastman Ia-O, which is fast and very contrasty, but has bad grain. The spectra are greatly widened and this removes much of the difficulty usually caused by poor grain. It is surprising

that we gain little when we used fine grain emulsions in our work with the Coudé. There are nine plates in all.

These have now been supplemented by nine more Coudé plates of exquisite quality from the Mount Wilson Observatory. We are exceedingly grateful to Dr. W. S. Adams for his generous offer to let us use his material in addition to our own. Finally, there are several visual Coudé plates by Swings, Henyey and myself, and also a good series of plates with the quartz Cassegrain spectrograph. The dispersion of the latter—all taken on Process emulsion—is 20 Å/mm at λ 3250. The work here has only recently been started but I can give a few preliminary results.

In the light of the review of available literature, which I have presented, we can now specify our problem. We have been given ample evidence that α Can Ven is a very peculiar star. There are some others like it—mostly discovered at Yerkes Observatory by Mr. Morgan—but concerning these other stars we know even less. An attempt must obviously be made to study in detail those which have already been discovered, for example, 73 Draconis, BD - 18°3789, θ Aquilae, ϵ Ursae Majoris,²³ and others; at the same time a fruitful field of endeavor would consist in the discovery of more objects having variable lines and in determining their periods. We may not be able to solve the mystery of these stars completely until we have enough material to apply statistical considerations. But that must wait until some one has the ability, skill and interest to undertake this work.

At present we shall have to limit our search for important new facts upon which to build a theory of those peculiar A stars to α Can Ven, their classical representative. In this connection we are quite naturally led to ask the following questions:

1. Granted that the rare-earth element europium has been identified with strong, variable lines in α Can Ven, what is the degree of certainty with which we have identified other rare earths? Kiess thought he had found *Tb* II, which was refuted by Morgan. Morgan says that *Dy* II and *Gd* II are quite strong, but Tai specifies his confirmation of *Dy* II with the words "seems to be unquestionable." He thinks that *Ce* II, *Tb* II and *Sa* II are "probably pres-

¹⁹ *Observatory*, 62, 219, 1939.

²⁰ *Op. cit.*

²¹ *Op. cit.*

²² *Contr. McDonald Obs.*, No. 13, 1939.

²³ Perhaps the most remarkable of these stars is ϵ UMa. Variable line intensities, especially of *Ca* II K, were discovered by Guthnick (*Sitz. Ber. Preuss. Akad. Wiss.*, 1931, p. 618; 1934, p. 13). The period is 5.0887 days.

ent," while for the other rare earths the evidence is described as insufficient. In another place he says that "the presence of *Sa* II . . . must be regarded as rather doubtful." It is obvious that on plates of small dispersion the positive identification of these and other rare earths will always remain difficult or even impossible. The high dispersion of the Coudé lends itself admirably to the solution of this question. Of course we must also look for other elements—not only the rare earths.

2. We next inquire: Do the radial velocities of the *Eu* II lines, as well as of other lines, really change, or are the variations reported by the early measurers solely due to blends, as Miss G. Farnsworth had thought?

3. Are there several groups of lines of variable velocity corresponding to the three intensity groups A, B and C?

4. Do all rare earths belong to group A, as Tai suggests by implication and, if so, are their variations alike in range and phase? How do the other elements vary?

5. Are the measurements of equivalent widths (E. W.) by Tai sufficiently reliable to serve as a basis for the computation of ionization phenomena, such as he has carried out?

6. Can normal changes in ionization, as postulated by Tai, account for the observational data?

7. Can we deduce anything from the fact that the lines of rare-earth elements are stronger than we had thought likely for an A-type star? Does this necessarily mean an exceptionally high abundance, as Tai has stated?

8. Does the high dispersion of our plates help us to find something significant in regard to the contours of the lines?

9. How does all of this tie in with the interpretation of the changes in α Can Ven and what are we to make of the hypotheses advanced by former workers?

10. Finally, what can we deduce from those peculiarities of α Can Ven, such as the weakness of *Ca* II, which it shares with many other A-type stars?

Our answers are preliminary in character, and may have to be revised after the work has been completed. But they will help us in trying to understand the nature of α Can Ven.

1. We start with the identifications. This part of the work is now under way and I can give some of the results. I have measured somewhat more than 1,000 lines between λ 3920 and λ 4670.

There are some 650 lines in Swings' measurements between λ 3000 and λ 3930. I shall probably add some 400 new lines from the ultraviolet Coudé plates from Mount Wilson. Perhaps some 500 lines will come from the visual region. In all we shall have 2,500 to 3,000 lines—quite a catch for an A-type star. In α Cygni we measured less than one-half this number.

My present identifications are all based upon the measurements of the McDonald plates. We note at once that *Cr* II and *Mn* II are relatively very strong, while *Fe* II, *Ti* II, and *Sr* II are average and *Sc* II and *Ni* II are very faint. *Si* II is exceptionally strong, and *Ca* II is exceptionally weak. When I use the word "relatively" I mean that the intensities are compared with some sort of standard of relative intensities of these elements as observed in "normal" A stars, such as α Cygni, α Lyrae, or α Can Maj.

Let us write these elements in order of increasing relative strength and add the corresponding ionization potentials and excitation potentials:

Element	I.P.	E.P.
<i>Ca</i> II	11.8 V	0 V
<i>Ni</i> II	18.2	3
<i>Sc</i> II	12.8	0-0.3
<i>Fe</i> I	7.8	0-2
<i>Fe</i> II	16.5	2-3
<i>Ti</i> II	13.6	1
<i>Sr</i> II	11.0	0
<i>Mn</i> II	15.7	2
<i>Cr</i> II	16.6	2-3
<i>Si</i> II	16.3	10

There is no correlation with either ionization or excitation potential. The plate to which I refer is one at which *Eu* II is strong, but that makes no difference because these elements all vary little and the order would remain the same if we had chosen another phase.

But most of these lines belong to the groups of lines which vary little or not at all. We are more interested in the unusual elements, such as the rare earths. The evidence is exceedingly interesting. The wave lengths are, of course, accurate to within one or two hundredths of an angstrom for sharp, single lines. For faint lines the errors are larger, but rarely exceed 0.05 Å except when there are blends. Moreover, we have at our disposal enormously more lines than any of the previous workers. Tai used some 270 lines.

I find many new lines of *Eu* II; the limit is around laboratory intensity 15, when 5,000 is the laboratory intensity of λ 4205 and 5 or 6 its stellar intensity near maximum. There are virtually hundreds of lines of *Gd* II and especially *Ce* II.

Dy II is certain with numerous coincidences; so is *Nd* II, which is completely new. *Sa* II is certain, also with numerous unblended lines. *Ho* II is represented by only one line. But it is almost certainly real. I have not carefully examined *La* II, but I think it is also present. There has been no time to examine *Tb* II, *Pr* II and the less satisfactorily known elements *Er* II, *Tm* II, *Yb* II, *Lu* II. The pertinent data (which include those of Tai) for the rare earths are shown in Table I.

TABLE I

Element	At. No.	Atomic Wt.	First Ion. Potential	Second Ion. Potential	Presence in α Can Ven
Lanthanum	57	138.9	5.6 V	11.5	Present
Cerium	58	140.1	6.5	—	Present
Praseodymium	59	140.9	5.8	—	?
Neodymium	60	144.3	6.3	—	Present
Illinium	61	—	—	—	?
Samarium	62	150.4	6.5	11.4	Present
Europium	63	152.0	5.6	11.2	Present
Gadolinium	64	157.3	6.2	—	Present
Terbium	65	159.2	6.7	—	Probably present
Dysprosium	66	162.5	6.8	—	Present
Holmium	67	163.5	—	—	Probably present
Erbium	68	167.6	—	—	?
Thulium	69	169.4	—	—	?
Ytterbium	70	173.5	7.1	—	?

The rare earths account for a large number of lines. But there remain several hundred unidentified lines, some of them strong. This is undoubtedly the largest, if not the most important, unexplored domain of stellar spectroscopy.

2. We proceed with the next question, namely, that of the radial velocities. I want to subdivide this question into three sections:

(a) Do the normal, strong group-C lines show velocity changes?

(b) Do the *Eu* II lines change in velocity?

(c) Is the velocity of *Eu* II when at maximum equal to that of the normal strong group C lines? To answer (a), I have accurately measured three lines: *Si* II 4128, *Si* II 4131, and *Fe* II 4233. The results are summarized in the following list:

Phase	No. of Plates	Mean Velocity of Strong <i>Si</i> II and <i>Fe</i> II Lines
-0.04	1	+1.7
+0.50	1	+0.7
+0.98	1	+0.2
+1.48	2	+1.8
+2.58	1	-0.3
+3.51	2	-0.5
+4.52	1 (adopted)	0.0

The total range is only 2.3 km/sec, which is probably not beyond the range of the possible errors of measurement or of the plates. There may be a suggestion that positive values predominate in the first half and negative in the second. It is safer, for the present, to suppose that these lines are stationary.

Since we probably can no longer believe that the lines of different groups come from different stars, we must suppose that the star is not a binary, but has a constant velocity. We turn to section (b). I have chosen *Eu* II 4205 and measured it accurately at those phases at which I can be certain that blends are entirely negligible. This precaution eliminates the doubt expressed by Miss Farnsworth.

Phase	Velocity of <i>Eu</i> II 4205
-0.04	+9.0
+0.50	+14.6
+0.98	+22.4
+1.48	+28.4
+2.58	too faint
+3.51	too faint
+4.52	0.0 (adopted)

The progression is very definite and places beyond any doubt the reality of the smoothly ascending curve, beginning one day before maximum intensity of *Eu* II and ending near phase 1.48 days, where the line becomes too weak to be measured. I have plotted the results on Kiess' curve, assuming a zero point at phase 4.52 which agrees with his velocity at minimum. My measures were relative and give no absolute values. The agreement is perfect.

Finally, we test section (c). I have measured only one plate completely, namely, that at phase 4.52 days. We select four lines, two of *Fe* II, two of *Si* II, and two of *Eu* II.

Line	Group	λ Measured	λ Laboratory	$\Delta\lambda$	Mean $\Delta\lambda$
<i>Fe</i> II	B	4205.262	0.480	-0.218	-0.222
<i>Fe</i> II	B	4233.942	0.168	-0.226	
<i>Si</i> II	C-B	4127.809	0.049	-0.240	-0.266
<i>Si</i> II	C-B	4130.590	0.882	-0.292	
<i>Eu</i> II	A	4204.639	0.046	-0.407	-0.366
<i>Eu</i> II	A	4129.412	0.737	-0.325	

The difference

$$\begin{aligned} \text{Eu II} - \text{Fe II} &= -0.144 \quad \text{or} \quad -10.2 \text{ km/sec} \\ \text{Eu II} - \text{Si II} &= -0.100 \quad \text{or} \quad -7.1 \text{ km/sec.} \end{aligned}$$

The difference is definite and real, but is appreciably smaller than that found by Kiess (-17 km/sec) or even by Belopolsky, who finds:

Fe, *Mg* -0.3 km/sec

Si II -5.8 km/sec

Eu II at minimum velocity -18 km/sec.

It is true, however, that my plate was taken at phase -0.95 day counted from maximum of *Eu* II intensity, while minimum velocity on Kiess' curve falls 1.6 days earlier than maximum intensity.

We conclude that *Eu* II has a negative displacement before phase zero and a positive after phase zero. This may be due to real motion or to lack of symmetry of the contours. The plates themselves show no such asymmetry in $\lambda 4129$, which is free of blends. It is probable that the velocities represent real currents within a stationary atmosphere.

Miss Farnsworth's conclusions in regard to blending may apply to certain lines, but are not true of the strong lines of *Eu* II. It is, however, not clear why her velocity curve for $\lambda 4205$ ranges from 0 to about 30 km/sec, while that of Kiess goes from -20 to $+15$ km/sec. Slow changes may be present, but it is perhaps also possible that some error in the adopted procedure displaced her curve.

3. This question has already been answered in the affirmative. Whether all rare earths or, say, all lines of group A share the behavior of *Eu* II, I am not yet prepared to say.

4. I believe we can state from the preliminary identifications that the rare earths do, generally, belong to group A. But the range of variation in intensity is not the same for all elements. *Eu* II, *Nd* II and *Dy* II lead (A! in my designation), while *Gd* II, *Sa* II and *Ce* II have smaller ranges (A or sometimes C, especially for the fainter lines). Otherwise, there are also conspicuous differences in the range of variation. *Cr* II is conspicuously B! while *Fe* II is B and *Si* II is either C or B. In general, my results agree with those of Tai. *Ti* II is slightly A, *Ca* K is almost constant, as is *Mg* II 4481. *Fe* I is slightly, but definitely, of group A. There can be no doubt that the rare earths distinguish themselves only by the fact that *Eu* II, *Dy* II and *Nd* II are most conspicuously A!, but the tendency to change in phase with these elements is shared by others which are not rare earths.

5. We have here only a few preliminary data from one plate near *Eu* max. (phase -0.09 day)

and two near *Eu* minimum (phases 1.5 and 3.5 days). The results for *Eu* II 4129 are

Phase	No.	Equivalent Width
0 day.....	(1)	0.15 Å
2 days.....	(2)	0.02 Å

At minimum the line is invisible, and the ratio *S* of the equivalent widths (in Tai's designation) is at least 10. He uses 3 in his computations of ionization. Moreover Tai found at maximum 0.3 Å and at minimum 0.1 Å for $\lambda 4129$, or 2 and 5 times the values found here.

6. The procedure adopted by Tai consisted of the following steps:

(a) He attributed the great strength of the rare earths at maximum to unusually large abundance.

(b) He noticed that, in general, there appeared to be a tendency for elements of low ionization potential to belong to group A and of high ionization potential to group B.

(c) He chose *Eu* II for group A and *Ti* II and *Fe* II for group B.

(d) He assumed that the observed ratio $S = \frac{\text{E.W. at max.}}{\text{E.W. at min.}} = \frac{1 - x_1}{1 - x_2} = 3$.

(e) He computed under various assumptions of pressure and temperature changes the corresponding values of *S* and compared them with the observed values *S*₀ for *Ti* II and *Fe* II, after applying corrections for excitation by the Boltzmann formula.

(f) He chose as best fitting a change in *p* by a factor of 2 and in *T* from 9,000° to 10,000°.

(g) He acknowledged the fact that for *H*, *Si* II, *Mg* II, *Ca* II, *Sr* II, *Zr* II, *Y* II the same change in conditions would assign the lines to the correct group, but would predict a larger change in intensity than that observed.

(h) He concluded "we can then explain the spectral change in terms of thermal ionization and excitation."

If this were so, the problem would be relatively simple. But can we really invoke thermal ionization? The crucial point lies in the behavior of other elements than those considered by Tai:

(a) The ionization potential of *Sr* II is 11.0 volts. That of *Ca* II is 11.8 volts and that of *Eu* II is 11.2 volts. The lines of all three elements are ultimate, arising from the ground level. Computation by means of the ionization equation

shows that $S = \frac{1 - x_1}{1 - x_2}$ for *Sr* II must be even

greater than for europium. We found for the latter $S \geq 10$. Yet, the strontium lines change very little in intensity, if at all. The discrepancy between *Sr* II and *Eu* II is much more significant than the agreement between *Eu* II and *Ti* II. It completely rules out an interpretation of the phenomena of variation in terms of the simple theory of thermal ionization. This does not mean that the theory is incorrect, nor that the theory has no application in the case of α^2 Can Ven. But it does mean that the observed phenomena are influenced by factors which are not encompassed within the scope of Saha's equation.

(b) The fact that S is probably greater than 10 for *Eu* II, instead of 3, as assumed by Tai, necessitates much larger changes in pressure or temperature, or both, than Tai had proposed. It is extremely doubtful that such major changes, for example one in temperature of the order of $2,000^\circ$, could take place without producing a much greater variation in light than the 0.03 mag. actually observed. Roughly speaking, the light changes as the fourth power of the temperature. A change from $10,000^\circ$ to $12,000^\circ$ should give us a photometric range of

$$2.5 \log \left(\frac{12,000}{10,000} \right)^4 = 0.8 \text{ mag.}$$

with maximum light when *Eu* II is weakest. In reality, the range is 0.03 mag., and the maximum of light occurs when *Eu* II is strongest.

(c) It is highly doubtful whether the observed ratio of equivalent widths can be identified with the ratio $S = \frac{1 - x_1}{1 - x_2}$ of the numbers of singly-ionized atoms. We know that in nearly all stellar spectra the curve of growth is such that the equivalent widths increase much slower than the corresponding numbers of atoms. For all but the very faintest lines a good approximation is

$$\text{E.W.} \sim \sqrt{N H f}$$

and

$$\frac{(\text{E.W.})_1}{(\text{E.W.})_2} = \sqrt{S}.$$

This makes our lower limit $S = 100$ for *Eu* II, and the corresponding changes in the physical conditions are even more extreme. We conclude that our answer to question 6 is "No."

7. The "rare earths" are, of course, relatively rare elements, but their abundances are not so small as to exclude their presence in stellar spec-

tra. The important factor is the large number of levels which distribute the energy among many lines. Among the A-stars the temperature is so high that the ionization is nearly complete. Tai computes for *Eu* II at $p = 10^{-4}$ atmos., $T = 10,000^\circ$:

$$\frac{x_1}{1 - x_1} = 83,$$

so that most of the atoms are doubly-ionized. It is, indeed, a fact that *Eu* II normally occurs in types F and G and we may assume that it reaches its normal maximum in these types. The strong lines in α Can Ven and other peculiar A stars are definitely abnormal.²⁴ They may be due to

- (a) high abundance,
- (b) suppression of double ionization,
- (c) a special mechanism of line production such as may be caused by stratification.

We exclude from consideration (a) because there is not much that can be said about it. We have already seen that the large range in variation of *Eu* II is not due to normal changes in the physical conditions. Unless we are willing to think in terms of creation and destruction of *Eu* atoms, we cannot account for the great intensity of these lines at their maximum. At minimum there is not much to be explained. I doubt that (c) can account for the variations. At any rate, the relative weakness of those *Eu* II lines which lie in the ultraviolet and are within the wings of the Balmer lines suggests that the level of the *Eu* II lines is not unexpectedly high.

We are left with mechanism (b)—a variable degree of suppression of double ionization. Incidentally, various abnormalities caused by cycles within the *Eu* II spectrum are excluded because those lines which come from normal, not metastable, levels show corresponding intensities and variations. There is no appreciable geometrical dilution. Similar conclusions apply also to the other rare earths.

8. We find that the contours of the lines of groups C and B are somewhat broader, as if affected by greater turbulence or greater rotation, when the *Eu* II lines are weak. The significance of this result is not yet clear.

9. I believe that in the present stage of the work it is best to explore the hypothesis that small changes occur in the physical conditions which

²⁴ Morgan, *Ap.J.*, 75, 53, 1932.

bring about large changes in the observed intensities. Such an effect is not possible when the physical conditions are similar to those of thermodynamic equilibrium. But we must remember that the Lyman lines and the Lyman continuum must be tremendously strong. The energy density which affects the ionization of the various elements is not that of a black body, and all kinds of departures must be important. Since all rare earths are of group A we are tempted to prefer an explanation in terms of abundance. But we must remember that the second ionization potentials of the rare earths are probably very similar. Hence it is not surprising that they behave in a somewhat similar manner. Whatever the agent may be that suppresses the second ionization of the rare earths at ionization potentials of 11.2 to 11.4 volts, it does not appreciably affect *Sr* II with ionization potential 11.0 volts or *Ca* II with ionization potential 11.8 volts. A strong absorption feature between 11.2 and 11.8 volts would perhaps answer the purpose, but in that case only a variation in the intensity of this feature could produce the variability of the observed line intensities. Perhaps there are other effects which can produce similar results. The motions of approach prior to intensity maximum and of descent following it suggest some type of selective radiation pressure with conversion of ionization energy into kinetic energy. The nature of the process remains obscure, but the fact that thermodynamic equilibrium is far from being applicable undoubtedly permits the mechanism to operate.

Incidentally, the *Eu* II line λ 4205 in δ Cephei seems also to be very sensitive to changes in intensity, and it certainly looks as though the phenomenon is similar to that observed in α^2 Can Ven.²⁵

10. The proximity of the ionization energy of *Ca* II to L_β suggests that for this line the ionizing radiation may come, to an appreciable extent, from a bright chromospheric L_β line. This hypothesis would permit us to divide the A-type stars into two groups: those with pronounced chromospheres, in which *Ca* II is super-ionized,

and those without chromospheres, in which *Ca* is under-ionized. This hypothesis has the advantage of shifting the responsibility for the variations in *Ca* II (as in ϵ UMa) to a chromospheric variation, which is *a priori* more probable than a large variation in pressure and temperature of the reversing layer. Swings and I have dealt with this hypothesis in another paper.

One other feature remains to be pointed out: the Balmer lines of *H* in α Can Ven are always appreciably weaker than in other stars of similar spectral type²⁶ and, according to Barbier, Chalonge and their collaborators, the Balmer jump in the continuous spectrum is nearly one-half of that observed in normal A0 stars.²⁷ But the Balmer lines are broad and the Stark effect is as conspicuous as in normal main-sequence stars. Low abundance of *H* may be the explanation, but it is difficult to see how this could reduce the intensity of *Ca* II and increase that of the rare earths. The *H* lines belong to group B, and are, therefore, weakest when the *Eu* II lines are strongest. But the change in equivalent width for *H* is not nearly as large as for *Eu* II.

It would be too optimistic to say that Cor Caroli has finally given up its secret. But I think we have accomplished two things: we have removed the problem from the list of astronomical mysteries, tinged by the superstition that Cor Caroli stands alone among the stars and by the naive belief that some sort of almost supernatural phenomenon gives rise to the creation and destruction of atoms of rare earths in a period of 5.5 days. On the other hand, we have been led to conclude that the other extreme of previous explanations, namely, in terms of the simple theory of thermal ionization, is equally dangerous because it obscures the most interesting and exciting characteristics of the star. We have suggested how the phenomena might be explained, and in doing so we have shown the way by which we shall travel toward our goal, the interpretation of the spectroscopic anomalies of α Can Ven.

²⁵ See especially Plate XVI, *Ap.J.*, 90, 1939.

²⁷ *Ann. d'Ap.*, 2 and 4, 1938.

²⁶ Krieger, *Ap.J.*, 79, 98, 1934.

A COMPARATIVE STUDY OF GRAHAMELLAE, HAEMOBARTONELLAE AND EPERYTHROZOA IN SMALL MAMMALS

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TABLE OF CONTENTS

	PAGE		PAGE
I. INTRODUCTION.....	359	<i>Haemobartonella peromysci</i> , new species, of the	
Primary Classification.....	359	Local Deer Mouse.....	377
Grahamellae, haemobartonellae, eperythro-		Infectivity for Other Species, Pathogenicity,	
zoa.....	360	Effect of Foreign Host on Morphology.....	377
Criteria for the Differentiation of Species.....	360	<i>Haemobartonella peromysci maniculati</i> , new	
Material and Methods.....	360	variety, of the Gray-backed Deer Mouse.....	381
Effect of Splenectomy upon Infection.....	360	Infectivity, Pathogenicity.....	382
Incidence of Infections, Table 1.....	361	<i>Haemobartonella blarinae</i> , new species, of the	
II. THE <i>Grahamellae</i> OF VARIOUS SMALL MAMMALS,		Short-tailed Shrew.....	382
AS OBSERVED IN BLOOD AND IN CULTURES		Growth from Spore-like Bodies and Branching	
Cultivation.....	362	<i>Haemobartonella sciuri</i> , new species, of the Gray	
<i>Grahamella peromysci</i> , new species, of the Local		Squirrel.....	385
Deer Mouse.....	363	Prominence of Coarse Bead-like Forms.....	385
<i>Grahamella peromysci maniculati</i> , new variety,		Indications as to the Systematic Position of the	
of the Gray-backed Deer Mouse.....	365	<i>Haemobartonellae</i>	386
<i>Grahamella microti pennsylvanicus</i> , new variety,		IV. <i>Eperythrozoo</i> OF SMALL MAMMALS	
of the Common Vole.....	366	<i>Eperythrozoon</i> Infections of the Common Mouse	
<i>Grahamella blarinae</i> , new species, of the Short-		and of the Local Vole.....	387
tailed Shrew.....	370	<i>Eperythrozoon varians</i> , new species, of the Gray-	
<i>Grahamella phylloides</i> , new species, of the		backed Deer Mouse.....	387
Peruvian Field Mouse.....	371	V. GENERAL CONSIDERATION	
<i>Grahamella</i> species ? of the Pine Mouse.....	372	Purity of Infections and Cultures.....	389
Other Organisms Isolated in Culture from the		Host Specificity of <i>Grahamellae</i> , <i>Haemobarto-</i>	
Blood.....	372	<i>nellae</i> , and <i>Eperythrozoo</i> , Table 2.....	390
General Features and Systematic Position of		Interference Phenomenon in Associated Infec-	
<i>Grahamellae</i>	374	tions, Table 3.....	390
III. <i>Haemobartonellae</i> OF SMALL MAMMALS		Comparison of Biological Characters of <i>Gra-</i>	
<i>Haemobartonella microti</i> Tyzzer and Weinman,		hamellae, <i>Haemobartonellae</i> and <i>Eperythrozoo</i>	393
1939, of the Common Vole.....	376	Summary.....	396
Failure of Attempts to Cultivate.....	376		

I. INTRODUCTION

In a previous study of the blood infections of the field vole, *Microtus pennsylvanicus pennsylvanicus*, attention was called to certain characteristics of the bartonellae of small mammals, differentiating them from *Bartonella bacilliformis* of the human being, and the genus *Haemobartonella* was created to include them (Tyzzer and Weinman, 1939). A question was raised as to whether the haemobartonella of the vole might assume a grahamella-like distribution in relation to the red blood corpuscles during certain phases of infection, not only in its natural host, but also in white mice inoculated with blood of infected voles. Subsequently, it was felt that certain

conclusions in regard to the purity of the vole infection studied were open to question, and on this account a further investigation of the subject has been undertaken. The evidence now at hand indicates that we were dealing with a mixed infection and that the occurrence of rods distributed within the red blood corpuscles was due to the presence of a species of grahamella. The present study has, furthermore, brought out certain additional features of interest in regard to grahamellae, haemobartonellae, and eperythrozoo.

Primary Classification

The three types of organism under consideration may be distinguished on the basis of mor-

phology, their relation to the red blood corpuscles, reaction to splenectomy, reaction to arsphenamine, and ease of cultivation, these distinctions having been made through the combined contributions of various authors. Grahamellae as found in the blood present a marked degree of uniformity, appearing as rods with only an occasional rounded form, and are situated definitely within the red blood cells. They are not greatly increased by splenectomy, infect only a small percentage of the red cells, are not known to be pathogenic, are not eradicated by treatment with arsphenamine and are readily grown on certain media (Tyzzer, 1941). Organisms of this type stain readily and more intensely than some of the haemobartonellae.

The haemobartonellae exhibit great polymorphism, are distributed over the surfaces of the red blood corpuscles, are greatly increased by splenectomy and are often pathogenic for the splenectomized animal through the production of anemia. Organisms of this type differ from those of the genus *Bartonella* in that they show no evidence of multiplying in tissues other than the blood and do not produce cutaneous eruptions. They also may be eradicated by treatment with arsphenamine and, judging from the present study, are not readily cultured. Great differences are apparent in the haemobartonellae of various hosts in regard to their affinity for stains.

The eperythrozoon present a variety of forms, usually with a large proportion of ring-like elements, and occur on the surface of the red cells and in the blood plasma. They react to splenectomy and to arsphenamine as do the haemobartonellae and have not been grown in culture.

The criteria for the recognition of species of the genera, *Grahamella* Brumpt, 1911, *Haemobartonella* Tyzzer and Weinman, 1939, and *Eperythrozoon* Schilling, 1928, are rather meagre. The custom quite generally followed of differentiating species of organism primarily on the basis of host of origin implies a high degree of host specificity. From the ease with which certain of the haemobartonellae may be experimentally transferred to unrelated hosts, it seems at least possible that some such organisms may be encountered in more than a single host species in nature and also that more than one species of a type may be found in a single host species. However, there is at present no positive information in regard to either of these questions. Pathogenicity may increase during successive passages

in a foreign host according to Adler (1930) who reported that *H. muris*, at first innocuous for non-splenectomized mice, later, after repeated passages became pathogenic. Hence it would appear that pathogenicity may not be regarded as a stable character. Other criteria to be considered, in addition to host of origin, are infectivity for various hosts, which may be taken as a measure of host specificity, morphology, pathogenicity, as indicated by blood changes and symptoms, and cultural characteristics if grown in culture.

There is in general no clearly distinctive morphology in the grahamellae of the various hosts studied. Ease of cultivation on artificial media not only sets the grahamellae off from the haemobartonellae but differences in growth characteristics support the differentiation of species, heretofore based on host of origin. The haemobartonellae often show no great degree of host specificity and are not readily propagated in culture so that—aside from the host of origin—morphology and infectivity or pathogenicity for various hosts are about the only criteria for the differentiation of species. In eperythrozoon, host of origin, infectivity for different hosts and morphology appear to be at present the only characteristics upon which species may be based.

Material and Methods

Infections of the three types of organism under discussion are found in trapped native mammals of various species. Grahamella infections are often apparent in non-splenectomized animals on examination of Giemsa-stained blood films. Splenectomy usually serves for demonstrating the presence of haemobartonella and eperythrozoon infections, and while the failure of splenectomy to make these infections apparent in the trapped animal furnishes grounds for assuming it to be non-infected, negative findings in regard to grahamella are much less conclusive. Rare infected red cells, found on a given date, may not be again demonstrable over a period of many weeks. The susceptibility of trapped animals without any demonstrated grahamellae in the blood to experimentally induced infection furnishes strong evidence as to their previous freedom from grahamella infection, while non-susceptibility may be based on immunity resulting from previous infection. The employment of laboratory-reared animals in experimental work such as that undertaken presents obvious

TABLE 1
INCIDENCE OF BLOOD PARASITES IN THE BLOOD OF SMALL MAMMALS FOLLOWING SPLENECTOMY

Animal*	Trapped†	Haemobartonella	Grahamella	Eperythrozoon
Vole	9714 Dec. 1939, Wakefield	0	0	0
	9812 Sept. 1940, Wakefield	+	0	0
	9825 Oct. 1940, Wakefield	+	+	0
	9826 Oct. 1940, Wakefield	+	+	0
	9827 Oct. 1940, Wakefield	+	+	0
Local Deer Mouse	9367 Aug. 1936, Martha's Vineyard	+	+	0
	9369** Aug. 1936, Martha's Vineyard		0	
	9675 Dec. 1939, Wakefield	0	0	0
	9680 Dec. 1939, Wakefield	0	0	0
	9682 Dec. 1939, Wakefield	+	+	0
	9683 Dec. 1939, Wakefield	+	+	0
	9699 Dec. 1939, Wakefield	0	+	0
	9700 Dec. 1939, Wakefield	0	0	0
	9701 Dec. 1939, Wakefield	0	0	0
	9702 Dec. 1939, Wakefield	0	0	0
	9764 Feb. 1940, Westboro	+	+	0
	9765 Feb. 1940, Westboro	+	+	0
	9766 May 1940, Wakefield	+	+	0
	9767** May 1940, Wakefield		+	
Gray-backed Deer Mouse	9817 Sept. 1940, Ossipee, N. H.	+	0	+
	9818 Sept. 1940, Ossipee, N. H.	+	+	+
	9819 Sept. 1940, Ossipee, N. H.	+	0	+
Pine Mouse	9732** Feb. 1940, Athens, Ga.		0	
	9736** Mar. 1940, Athens, Ga.		0	
	9738 Mar. 1940, Athens, Ga.		+	
Red-backed Mouse	9829** Oct. 1940, Harvard		0	
Mole	9729** Feb. 1940, Athens, Ga.		0	
	9734** Feb. 1940, Athens, Ga.		0	
Shrew	9815** Sept. 1940, Wakefield		+	
	9816 Sept. 1940, Wakefield	+	+	0
	9880 Feb. 19, 1941, Wakefield	+	0	
Gray Squirrel	9667 Nov. 1939, Norwell	+	0	0
"Peruvian Mouse"	9719 1936, Peru, S. A.	0	+	
	9720 1936, Peru, S. A.		+	
	9721 1936, Peru, S. A.		+	
	9722 1936, Peru, S. A.	0	0	

* Vole = *Microtus pennsylvanicus pennsylvanicus*; Local Deer Mouse = *Peromyscus leucopus novaboracensis*; Gray-backed Deer Mouse = *Peromyscus maniculatus gracilis*; Pine Mouse = *Pitymys pinetorum*; Red-backed Mouse = *Clethrionomys (Eutamias) gapperi*; Mole = *Scalopus aquaticus howelli*; Shrew = *Blarina brevicauda (talpoides)*; Gray Squirrel = *Sciurus carolinensis leucotis*; "Peruvian Mouse" = *Phyllotis darwini linatus*.

** Not splenectomized.

† Localities in Massachusetts, except when otherwise indicated.

‡ Infection became apparent 55 days after splenectomy.

advantages. Both voles and deer mice, reared under laboratory conditions with measures taken to eliminate ectoparasites, have proved to be free of all blood infections. The freedom of ani-

mals from haemobartonella and eperythrozoon has been checked by splenectomy, which has been done as a matter of routine, except for several animals injected with grahamella. For experi-

mental passage, a routine has been adopted of injecting non-infected animals both subcutaneously and intraperitoneally with the blood of an infected animal, suspended in normal saline or citrated saline solution. The elimination of certain organisms from a mixed infection may be accomplished in some cases by one or more passages in a foreign host, but this method for the isolation of a pure infection is not always reliable and should be carefully checked. Cultivation on artificial media is obviously advantageous, when possible. The accumulated experience in the cultivation of *Bartonella bacilliformis* has been utilized and many different media have been employed.

Morphological studies have been made in connection with each infection, blood films being prepared at frequent intervals and stained by the Giemsa method. Darkfield study has also been carried out, more especially of organisms grown in culture medium. There are complicating factors in the darkfield examination of infected blood and no new information has resulted from a limited number of observations.

The sources of the infections studied and some indication of their incidence are set forth in Table 1. Except in case of pine mice and moles and two grahamella-infected Peruvian mice in which only a single observation was made, repeated examinations of the blood were made at irregular intervals, an average of twelve blood films per animal being studied.

Most of the animals listed in the above table were splenectomized. In regard to those not splenectomized, we have no evidence as to the incidence of haemobartonella or of eperythrozoon, but such animals are included in order to indicate the incidence of grahamella.

For purposes of brevity, *Microtus pennsylvanicus pennsylvanicus* will be referred to in the text as the "vole," *Peromyscus leucopus novaboracensis* as the "local deer mouse" and *P. maniculatus gracilis* as the "gray-backed mouse." The semi-solid leptospira medium of Noguchi will be abbreviated to "leptospira medium." The question arises whether to follow precedent in describing the grahamella of each host as a separate species or to regard those of different hosts as adapted strains of a single species. The former alternative offers the advantage of providing a concise label for any future reference to a given organism. Hence, for purposes of identification and description, specific or varietal names will be applied to the organisms on the basis of host of origin, but

on account of the limited information in regard to such organisms, the nomenclature here adopted may be regarded as tentative.

II. THE *Grahamellae* OF VARIOUS SMALL ANIMALS, AS OBSERVED IN BLOOD AND IN CULTURES

Cultivation

In the course of attempts to isolate in culture the various haemobartonellae studied, the first definite growth was obtained in the semi-solid leptospira medium of Noguchi (Noguchi and Battistini, 1926), from a mixed grahamella and haemobartonella infection in the local deer mouse. This, at the time, was erroneously interpreted as the growth of the haemobartonella, was given only casual attention and not maintained. A second culture isolated from a similar mixed infection of another animal of the same species and carried through several passages in leptospira medium was employed four months later to inoculate two clean laboratory-reared deer mice which had been splenectomized. In one animal grahamella infection appeared in eight days, in the other, ten days after inoculation, and both remained free of any other infection. The organism was recovered in culture from the blood of both these inoculated animals two weeks after inoculation. With this evidence of the culturability of a grahamella, blood was taken from three trapped voles, each showing grahamella infection, and planted on various media. A pure culture of an organism growing in dense aggregates in semi-solid media was obtained from each. All three of these voles carried a latent bartonella infection as demonstrated subsequently by splenectomy. The inoculation of laboratory-reared voles with one of the culture strains was followed by grahamella infections. Subsequent splenectomy of the inoculated animals showed them to be free of any haemobartonella or eperythrozoon infection. An organism identical in character with that injected was isolated in culture from the blood of one of the inoculated voles.

An organism was grown in culture from the blood of a splenectomized gray-backed deer mouse showing a triple infection of grahamella, haemobartonella and eperythrozoon. This organism resembled rather closely the grahamella isolated in culture from the local deer mouse. The inoculation of two gray-backed mice and three local deer mice with culture material was followed by grahamella infection in all five ani-

mals. Three weeks after inoculation, blood from one of the local deer mice was planted on media and yielded a pure culture of the organism injected.

A short-tailed shrew, *Blarina brevicauda*, showing grahamella infection, also furnished growth on media inoculated with blood, which is probably that of the grahamella seen in the blood, but proof is lacking since no shrews known to be free of infection were available for test purposes. The above shrew after splenectomy developed a heavy haemobartonella infection. An organism was isolated in culture at this time identical with that obtained prior to splenectomy.

Thus, organisms isolated in culture from blood of two species of deer mice and of the common vole showing grahamella infections, have produced in turn grahamella infections when inoculated into other animals of the same species, and all three organisms have then been recovered in culture from the blood of the inoculated animals, thus fulfilling Koch's postulates. The employment of splenectomized animals for inoculation makes it reasonably certain that they carried no haemobartonella or eperythrozoon infection. It appears probable that the organism isolated from a mixed infection of grahamella and haemobartonella in the short-tailed shrew is also a grahamella, but in view of the frequency with which various types of organisms may be isolated from the blood of small mammals, this by no means should be assumed.

Grahamella peromysci, new species, of the Local Deer Mouse, *P. leucopus novaboracensis*

As seen in Giemsa-stained blood films, this grahamella possesses no features distinctive from grahamellae occurring in other host species examined.¹ In contrast to the variety of forms seen in the haemobartonellae, this organism shows rather uniform rods distributed within, rather than upon, the erythrocyte. Associated with the rods are occasional rounded coccoid forms which probably represent a developmental phase of the organism. The grahamellae are distributed throughout the red cell, characteristically lying apart from one another, the only

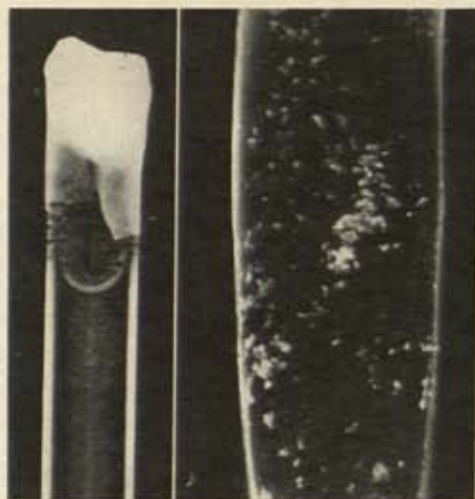


FIG. 1. Cultures of *Grahamella peromysci* of the local deer mouse. A. Growth in tryptose semi-solid medium. $\times 1$. B. Growth on blood agar slant, 20 days, $\times 2$.

exception being occasional paired rods interpreted as division forms. The grahamellae stain readily, often uniformly, but may show intensely stained granules. There is convincing evidence that the groups of extracellular grahamellae occasionally encountered in stained blood films are derived from infected red cells ruptured in the process of preparing the film.

Growth of this grahamella from blood planted in leptospira medium is first indicated by the development of minute, discrete, whitish particles appearing in from seven to ten days at 28° C., or after a longer interval at room temperature, 20–22° C. These particles increase in size and appear as irregular, sharply outlined white masses or flakes usually attaining their maximum development in a 5 to 10 mm zone² at the top of the medium. The initial flakes, evidently derived from a single infected red cell, never grow to more than 0.8 mm in diameter and from these dissemination occurs so that at a given time they may be surrounded by a cloud of satellite particles. With successive transfers of this organism, the tendency to particulate growth is largely lost and growth is indicated by the development of a zone of milky opacity at the top of the leptospira medium. By the inocula-

¹ In blood films of the European mole, showing *G. talpae* Brumpt, 1911, the type species of the genus, the organisms appear rather more intensely stained and of greater thickness than the grahamellae of local mammals, but since these preparations have been retained, it is possible that an excess of the dye has been deposited on the organisms.

² In order to photograph growths in semi-solid media, cultures of the various grahamellae were made in small flat tubes in which the characteristic subsurface zones did not develop. Allowance should be made for this in all the figures illustrating cultures in semi-solid media.

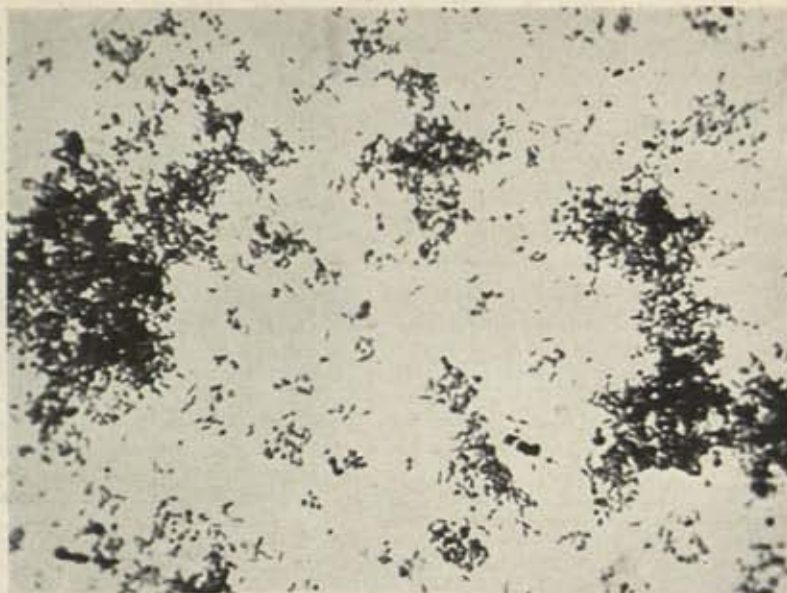


FIG. 2. Giemsa-stained film of *Grahamella peromysci* grown in semi-solid leptospira medium. Note rods, coccoid forms and larger globoid bodies. $\times 1275$.

tion of this medium with relatively few organisms the particulate type of growth may be made to reappear (Fig. 1 A). This organism grows well on slants of certain solid media in case the latter is moist and provided with an abundance of fluid at the bottom of the tube. Only slight growth is obtained on NNN medium, but on blood agar having an enriched agar base prepared according to the specifications of the American Association of Medical Milk Commissions, Inc. (1937), abundant growth occurs. In sparsely sown slants individual colonies appear which are at first transparent, later opalescent, somewhat flattened, button-like, varying in size but rarely attaining a diameter of more than 1.5 mm (Fig. 1 B). In the course of ordinary transfers the organism grows over the surface of the slant in a continuous sheet having an uneven pebbly surface. This sheet appears at first rather moist and glistening but in the course of weeks becomes somewhat dull in appearance. Uniformly good growth has been obtained with blood agar made up with rabbit, horse and sheep blood. Growth is not quite so abundant on media containing 5 per cent blood as on media containing 20 per cent blood, but is, nevertheless, satisfactory. With blood agar slants a film of growth is often found extending for a time over the surface of the water of condensation, but this later falls to the bottom so that there is eventually an

abundant, flaky deposit, which leaves the fluid wholly clear. Good growth is obtained on cystine blood agar and Bordet-Gengou medium when adequately moist. In peptone beef broth containing 2 per cent rabbit serum, *G. peromysci* forms a fine sediment at the bottom of the tube and the fluid becomes slightly clouded. In broth with hemoglobin, i.e. 2 per cent laked rabbit's corpuscles, the growth is more luxuriant and the fluid soon becomes clouded, while later a heavy precipitate forms and the medium assumes a dull brownish color. The organism, after becoming dispersed in fluid media, on transfer to leptospira medium, forms a whitish cloud without visible particles at the top of the medium.

G. peromysci, as grown on artificial media, presents a high degree of polymorphism and its morphology is obviously modified by the medium in which it is grown and the age of the culture. During early growth in leptospira medium the organism appears in compact clumps or aggregates of small elements, mostly rod-like in character (Fig. 2). Later the number of free organisms becomes progressively greater and coccoid forms and large globular bodies occur as well as rods. In media in which the organism occurs in aggregates, the peripheral portion of the organisms, as seen in Giemsa preparations, is tinted reddish and the outline is not distinct, while the central portion is deeply stained. Under conditions in

which the organisms are dispersed, as in old cultures and in peptone beef broth with hemoglobin, the organism assumes a more typical bacteriform aspect and presents sharply contoured rods and coccoid bodies, the former showing deeply stained granules often bipolar in position. During early cultivation there was scarcely any tendency to chain formation. After prolonged culture and on introduction to certain media, especially peptone beef broth with hemoglobin, the organism appears largely in chains or filaments with deeply stained granules at intervals (Fig. 13). The rods vary from 0.75 to 1.5 microns in length, rarely exceeding the latter figure. Such elements are slender, 0.25 of a micron in thickness when grown in leptospira medium and on blood agar, but when growing in chains in fluid media are from two to three times as thick. Coccoid forms vary from 0.25 to 1.0 micron in diameter. Globular elements also appear as the culture ages. These vary in size up to 10 or 12 microns, stain unevenly, and are frequently bluish in lightly stained Giemsa preparations.

As already noted, the inoculation of two laboratory-reared deer mice of the local species with this grahamella culture resulted in grahamella infection (Fig. 3) and the organism was recovered in culture from both inoculated animals.

Grahamella peromysci maniculati, wen variety, of the Gray-backed Deer Mouse, *Peromyscus maniculatus gracilis*

This organism, as it occurs in the blood of an infected animal (Fig. 6), is indistinguishable from that occurring in the local deer mouse. In culture it closely resembles the grahamella isolated from the latter animal but its initial growth was rather more luxuriant. In the primary growth on leptospira medium the initial granules attained large size, reaching a maximum about 1 mm in diameter, while in subsequent transfers in the same medium, growth is indicated by a milky zone 4 to 5 mm in thickness at the top of the medium. Examination with a hand lens reveals that the milky cloud is constituted of minute particles (Fig. 4 A and B). On slants of blood agar made up with the enriched agar base alluded to above, the growth is rather more luxuriant than that of the grahamella of the local deer mouse, and appears as a sheet with an uneven, slightly wrinkled surface, or as moist, rounded, button-like, opalescent colonies (Fig. 4 C). Abundant flaky deposit develops in the water of condensation.

In fluid media, this organism grows more profusely in the peptone beef broth with hemoglobin than in the same broth with 2 per cent serum. It not only forms an abundant, finely granular

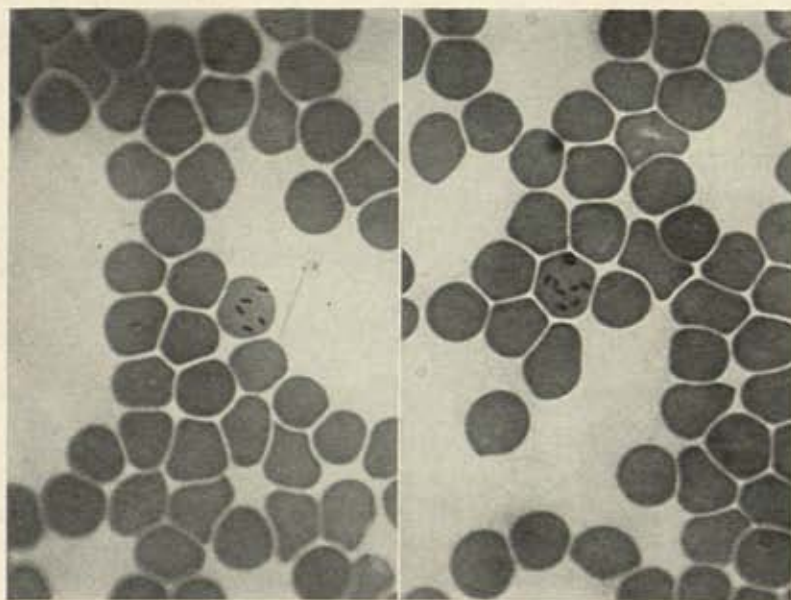


FIG. 3. Blood of laboratory-reared deer mouse of the local species, 11 days after inoculation of grahamella culture;—two red cells with typical grahamellae. Giemsa $\times 1275$.

sediment, but is distributed in small colonies adherent to the wall of the tube, these being larger and more abundant toward the top.

In Giemsa-stained films from cultures in leptospira medium, the organism occurs in dense aggregates and free forms, the latter consisting of delicate rods with tapering ends, and small coccoids (Fig. 5). In fluid medium, it grows in chains, but on transfer back to leptospira medium, the organism no longer shows any marked chain formation. This strain of organism, unlike the one from the local deer mouse, has maintained some degree of particulate growth in fluid media and does not become so markedly bacilliform in its morphological variation. Rod forms from leptospira and blood agar cultures vary from 0.75 to 1.75 microns in length by 0.25 micron in thickness. The chains growing in fluid media may be about three times as thick and coccoidal forms vary from 0.25 up to 1.0 micron in diameter.

Two trapped, gray-backed mice whose blood had not shown grahamella were inoculated with the organism grown in culture, and developed an infection of the red cells which became apparent fourteen days after inoculation. (See Table 3.) Two splenectomized local deer mice were also injected, one with blood of a gray-backed mouse showing a triple infection of haemobartonella, eperythrozoon and grahamella, the other with blood of a gray-backed mouse at the height of an

eperythrozoon infection. The first of the inoculated local deer mice developed a haemobartonellosis which alternated with an eperythrozoon infection, the other, a heavy eperythrozoon infection, but neither showed grahamella-infected red cells for seven weeks following the inoculation. Both animals were then injected with a culture of *G. peromysci maniculati* and showed infected red cells, one nine days, the other fourteen days later. A third laboratory-raised deer mouse of the local species was also experimentally infected by the injection on another occasion of a culture of the same grahamella, and showed infection twenty-two days after inoculation. Blood from one of the inoculated local deer mice planted on appropriate media gave growths of grahamella. Since this grahamella is infective for the local deer mouse, it may be regarded for the time being as a variety of *G. peromysci*.

Grahamella microti pennsylvanici, new variety,³ of the Common Vole, *Microtus pennsylvanicus pennsylvanicus*

Grahamella appears to be more frequently demonstrable in voles approaching maturity than

³ According to Yakimoff, 1929, *Grahamella microti* Lavie 1921 would appear to be preoccupied by *Grahamella arvalis* Tartakowsky 1913. However, the authenticity of Tartakowsky's species does not appear to be established. Yakimoff refers to the naming of the species in a catalogue of

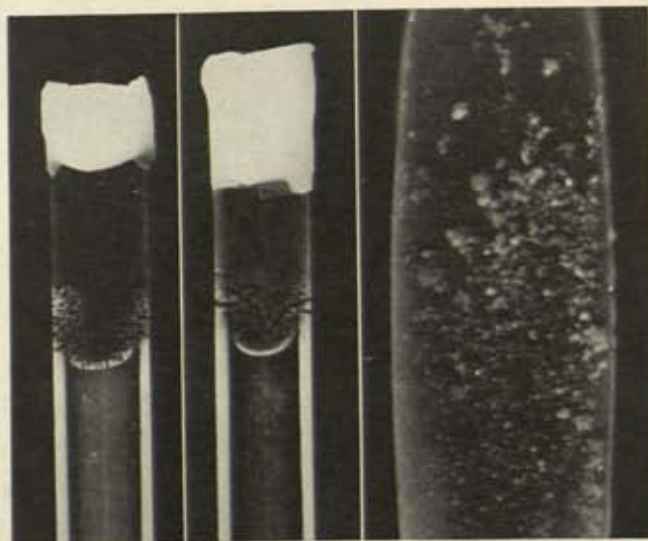


FIG. 4. Cultures of *Grahamella peromysci maniculati* of the gray-backed deer mouse. A. Leptospira semi-solid medium showing minute satellite granules spreading below coarser granules. $\times 1$. B. Tryptose semi-solid medium $\times 1$. C. Blood agar slant, 21 days. $\times 2$.

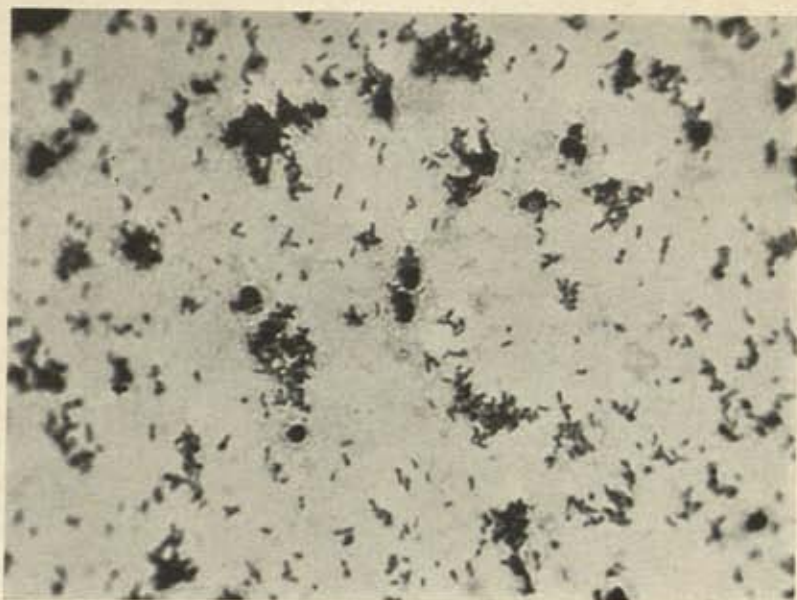


FIG. 5. Film from leptospira culture of *Grahamella peromysci maniculati*.
Giemsa $\times 1275$.

in old animals. The three culture strains isolated on one occasion from three trapped voles showing infected red cells appear to be identical, although only one has been tested out in compliance with Koch's postulates. Growth of the vole grahamella on various media shows one essential difference from the grahamella strains isolated from the two species of deer mice in its tendency to retain its particulate character in various media. In leptospira medium the organism grows in somewhat irregular, sharply outlined masses up to a millimeter in diameter, usually attaining greatest development in a layer up to 1 cm in thickness at the top of the medium (Fig. 7 B). In newly planted cultures particles may appear throughout the medium, but later the growth becomes more abundant toward the top and commonly constitutes an ill-defined zone of growth. On the blood agar slants growth appears in the form of definite colonies, never as a sheet (Fig. 7 C). With this grahamella the character of growth differs greatly with the con-

tent of the blood in the media irrespective of whether rabbit, sheep, or horse blood is used. While with 20 per cent blood growth continues and the colonies remain full and moist for a long period of time, with 5 per cent blood the growth of colonies proceeds for a relatively brief interval and is followed by regressive changes; the colonies become flattened, umbilicated, or umbonate, and have a dry, shriveled appearance. The regressing colonies commonly become iridescent and may present a peripheral zone of metallic, coppery-red color. The colonies of all three strains of the vole grahamella as grown on blood agar slants show great variation in type, not only in successive transfers but often in a single tube. The colonies may be classified as moist, translucent, conical; smooth, milky, low, button-like; and opaque, abruptly elevated, dimpled or granular. With such morphological differences, the possibilities of either the presence of more than a single species of organism in the culture or of dissociation within a single species were considered. With these questions in mind, single colonies of each type were picked and carried through a long series of transfers. No continuity of type was obtained but it was found that the type of colony depended upon the physical character of the inoculum, on the mode of inoculation, and on slight differences in the medium upon which it was planted. Thus, organisms

objects exhibited at an agricultural fair held in St. Petersburg in 1913. The validity of the species is contingent upon whether the name was accompanied by a description and whether it was effectively published, *i.e.*, printed or indelibly autographed and sold or distributed to the general public. (See International Rules of Botanical Nomenclature, Articles 36 and 37.) Since the catalogue in question is not at present available to the author, it is not possible to affirm Tartakowsky's species.

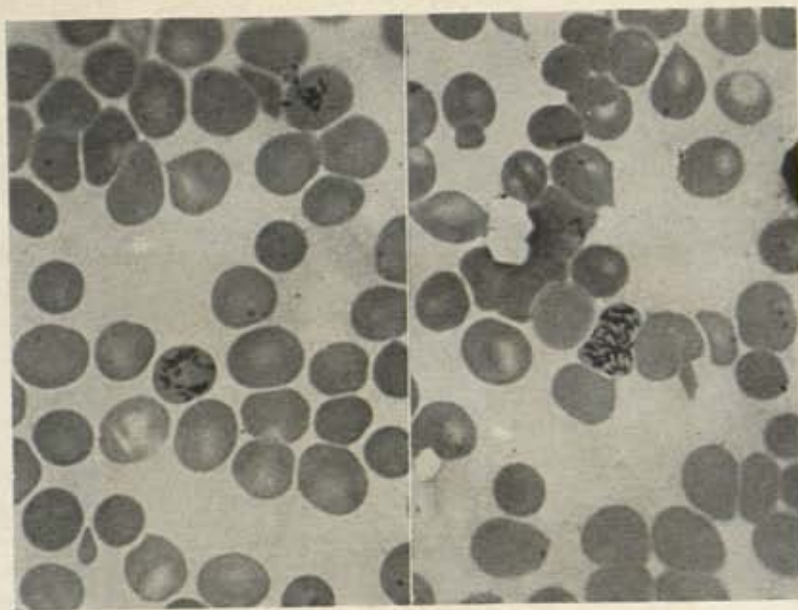


FIG. 6. Blood of splenectomized gray-backed deer mouse with mixed infection of grahamella and haemobartonella. A. Grahamellae within an infected erythrocyte and above and to right a group of grahamellae derived from a ruptured cell. B. A grahamella-infected red cell and above scattered rods and coccoid forms of haemobartonella. Giemsa $\times 1275$.

dispersed in fluid produced moist colonies on a moist medium, but deposited with leptospira medium on the blood agar slant produced opalescent, button-like colonies. The deposit of large aggregates or fragments of colonies furnishes dry, granular, or dimpled masses, often growing to great size. All types of colony are non-adherent and slip over the surface of the slant at the merest touch. The inoculation of leptospira medium with all types of colony furnishes growths which are identical in every respect. Giemsa-stained films of the various types of colonies show only a single type of organism. Hence it would appear that we are dealing with pure cultures in all three strains derived from the vole.

G. microti pennsylvanici grows in such dense, tough colonies that considerable manipulation is required in the preparation of films to obtain sufficient free organisms for study (Fig. 8). In fragments of colonies seen in Giemsa-stained films, the organisms appear to lie in a matrix by which they are cemented together in compact masses. The organism may be either rod-like or coccoid in form, the relative proportions of the two varying. Thus, after two weeks' growth on blood agar, the colonies may consist almost wholly of coccoid and globular forms, some appearing hollow or ring-like. With darkfield illu-

mination, a segment of a colony may present a rounded mass of coarse coccoid forms, while the remainder of the mass consists of rods. The latter average somewhat thicker than the rod forms of the deer mice. The rods show a range of variation, 0.7 to 2.7 microns in length, the thickness being quite constant, approximately 0.33 micron, and the coccoids vary from 0.33 to more than 1.0 micron in diameter. The rod forms commonly taper to the extremities, show a deeply stained central portion and a faintly stained peripheral portion, and are without a distinct contour. It is possible that the indistinct peripheral substance represents a secretion rather than an integral part of the organism, for under certain conditions this material is not apparent and the outline of the organism is well defined. In some preparations an excess of stringy mucoid material is encountered in which the organisms appear large and distorted as though flattened. The excess of external substance or matrix and the firm adherence in dense masses are outstanding features of the vole grahamella as grown in culture media.

Two young laboratory-reared voles with no organisms microscopically demonstrable in the blood were inoculated, one with organisms from an original culture twenty-three days after being

planted with blood, the other with organisms from the third transfer forty-seven days after isolation in culture. Both animals showed numbers of grahamella-infected red cells five days after inoculation, the cells at this stage of the infection showing relatively few organisms, *i.e.*

from one to four per cell. Blood from the second vole taken ten days after its inoculation furnished characteristic cultures on both leptospira and blood agar slants. The susceptibility of white mice to the vole grahamella was tested. Series of both splenectomized and young normal white

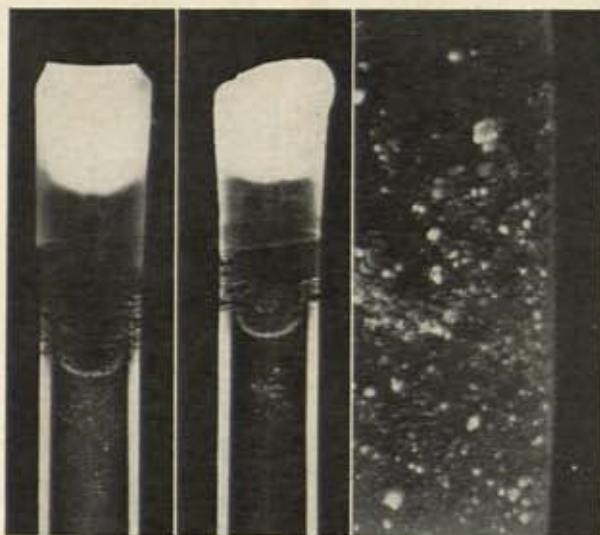


FIG. 7. Cultures of *Grahamella microti pennsylvanici* of the common vole. A. Leptospira semi-solid medium. $\times 1$. B. Tryptose semi-solid medium. $\times 1$. C. Blood agar slant 21 days. $\times 2$.

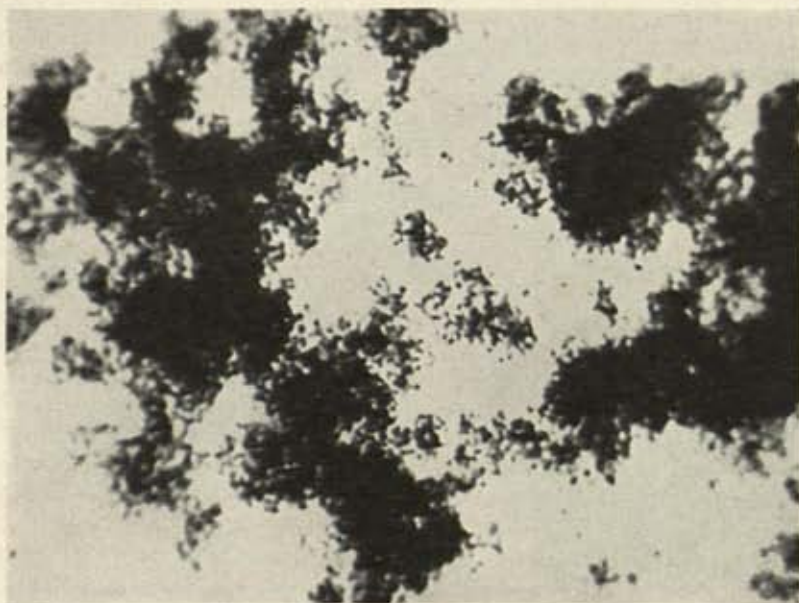


FIG. 8. Giemsa-stained film from grahamella culture derived from the blood of an infected vole. Note thickness of organisms and occurrence in compact masses. Semi-solid leptospira medium. $\times 1275$.

mice were injected with culture material, some being injected also with haemobartonella-infected vole blood, but no animal furnished any microscopic evidence of grahamella infection. The haemobartonellosis which resulted in two splenectomized mice inoculated with both cultured grahamella and bartonella-infected vole blood was carried through four successive transfers in splenectomized white mice. Although grahamella was never seen in blood films, it was isolated in culture from one of the first mice inoculated, twenty-four days after its injection, from the two mice of the next transfer seven and eleven days respectively after their injection, but all attempts at isolation from the mice of subsequent transfers failed. The cultures isolated from the inoculated mice have not been tested by the inoculation of voles as no laboratory-reared stock of these animals is now available, but on comparison of the organisms isolated with the strain of grahamella injected into the mice, all present the same type of growth on various media. Thus, it seems clear that the grahamella of the vole may persist in white mice when not microscopically demonstrable. On the other hand, it appears that on occasion the vole grahamella may multiply sufficiently on injection into the splenectomized white mouse to be microscopically demonstrable in the blood for a brief time, as shown in earlier experiments (Tyzzar and Weinman, 1939).

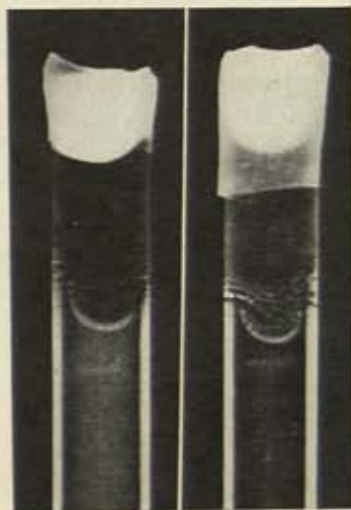


FIG. 9. Cultures derived from the blood of a short-tailed shrew, not tested by shrew inoculation. A. Leptospira semi-solid medium. $\times 1$. B. Tryptose semi-solid medium. $\times 1$.

Grahamella blarinae, new species, of the Short-tailed Shrew, *Blarina brevicauda*

The blood of two shrews, both taken in a trap set repeatedly in one locality, showed grahamella-infected red cells. One, kept for nearly three months in captivity, was splenectomized and subsequently developed a severe haemobartonellosis. Blood from the tail was taken both before and after splenectomy, and planted on various media. The same organism was isolated from blood taken on October 1 and that taken on November 6, splenectomy having been performed on November 1. While the organism grown (Figs. 9 and 10) resembled somewhat in its cultural characteristics the grahamellae isolated from the two species of deer mice, no laboratory-reared or demonstrably uninfected shrews have been available upon which to test the culture. The blood of the grahamella-infected shrew taken before splenectomy was used to inoculate two splenectomized deer mice, *P. leucopus novaboracensis*, and again after splenectomy, when the haemobartonellosis was at its height, to inoculate two splenectomized white mice. The subsequent examination of stained blood films of the inoculated animals taken over a period of several weeks gave no evidence of the transfer of infection. The injection of a young deer mouse of the above species with the organism grown in culture also resulted negatively. It was hoped that a third shrew trapped subsequently in a different locality might serve as a test animal, since its blood presented no grahamella-infected red cells. After being splenectomized with the possibility in mind of making apparent its latent infections, it developed a severe haemobartonellosis which was maintained throughout the period of nearly seven weeks for which it survived. No grahamellae were found in stained blood films taken at intervals throughout this period. Culture media planted with splenic tissue at the time of operation and a great variety of media planted ten days later with blood furnished no growth. On account of the unexpected death of this animal, the inoculation test for the organism previously isolated from shrew's blood was not carried out.

This organism in leptospira medium forms a milky cloud in a zone from 5 to 8 mm in thickness at the top of the medium. Examined with a hand lens, the zone shows minute, whitish particles in suspension, but there appears to be also a flocculation of the medium itself. On blood



FIG. 10. Giemsa-stained film of organisms isolated from blood of shrew;— from a colony on blood agar slant. $\times 1275$.

agar the organism grows in a sheet having a coarse, pebbly surface as though composed of confluent colonies of various sizes.

The organism cultured appears in the form of delicate rods from 0.75 to 2.3 microns in length by about 0.3 to 0.4 micron in thickness, which usually taper slightly toward the extremities, and may be slightly bent (Fig. 10). In some preparations the rods stain uniformly, presenting no granules, but usually a considerable proportion of the rods show a bead-like swelling, more frequently but not always centrally situated. Coccoid forms from 0.3 to 1.0 micron in diameter, and even coarser globules, occur. The larger globules stain bluish in lightly stained preparation and their origin is quite obviously from the swelling of rods, every stage of the process being apparent. Aggregates occur which are for the most part composed of such globules with a relatively small proportion of rods and coccoids. Under certain conditions of growth, the rods and coccoids may be dispersed and, as seen thickly distributed in the film, have a bacterium-like morphology. Usually the preparations show loose aggregates as well as free forms. In leptospira medium and on blood agar there is only slight tendency to form chains. This organism grows more profusely at 37.5° C. on blood agar slants than the three proved strains of grahamella; the medium turning a dull chocolate color.

Grahamella phyllotidis, new species, of the Peruvian Mouse, *Phyllotis darwini linatus*

Two of four trapped Peruvian mice presented grahamella infections peculiar in that the infected erythrocytes contained an unusually large number of organisms, in some instances so densely packed that the infected cell was intensely stained and resembled a nucleus (Fig. 11). In an attempted splenectomy both infected animals reacted badly to ether anesthesia and succumbed. Splenectomy was successfully performed on the two animals without visible infection and for a period of eleven days following the operation the blood of both showed no grahamellae. They

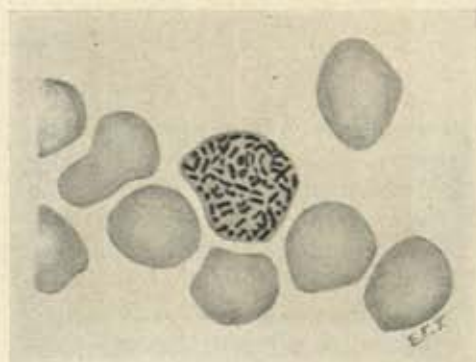


FIG. 11. *Grahamella phyllotidis*. Blood of Peruvian mouse, *Phyllotis darwini linatus*. Giemsa $\times 2000$.

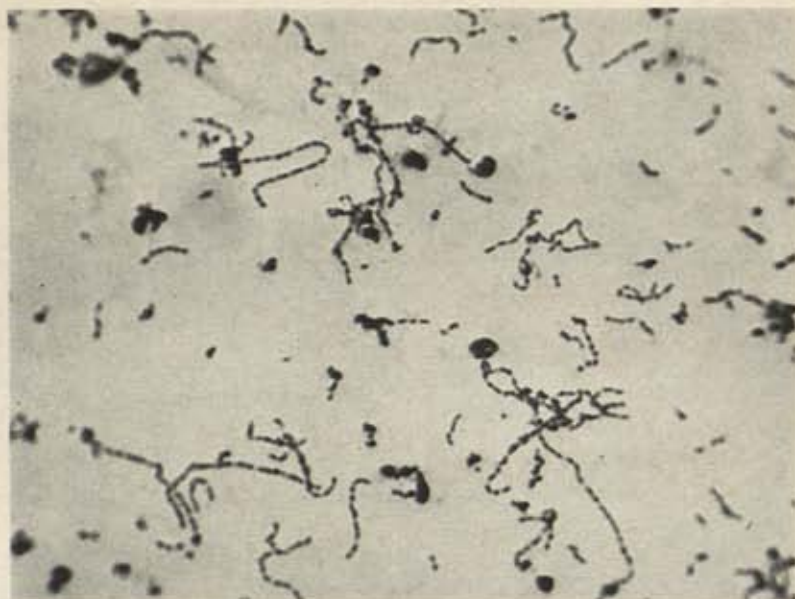


FIG. 12. Chain-forming organism isolated from blood of vole. Note large rounded bodies which appear early in development. *Leptospira* semi-solid medium. Giemsa $\times 1275$.

were then injected with the blood of a local deer mouse showing grahamellae, and six days later one presented numerous infected red cells. Many of these were well packed with rods, as was the case in the naturally infected *Phyllotis*, so that it is probable that the infection was a natural rather than an induced one. Two attempts to recover the grahamella in culture, in one case using tail blood, in the other heart's blood, yielded pure cultures of an organism growing in beaded filaments and forming loose aggregates of rods, coccoids and coarse spheroids in semi-solid media. The *Phyllotis*, showing no grahamella, also yielded the same organism. No clean stock was available for inoculation tests.

Grahamella species? of the Pine Mouse, *Pitymys pinetorum*

A grahamella found in the blood of a pine mouse trapped in Athens, Georgia, presents no distinctive morphology, being quite similar to the grahamella occurring in the vole and deer mice studied. The ground where the pine mice were trapped was tunnelled not only by these animals but also by moles of the species *Scalopus aquaticus howelli*, so that in this case as with other closely associated species of mammals, the possible sharing of a single species of grahamella by different host species may be considered. The

cultivation of the grahamella found in the pine mouse was not attempted. A splenectomized white mouse injected with blood of this pine mouse failed to develop a visible infection.

Other Organisms Isolated from Blood

In addition to the proved strains of grahamellae, several other possibly related organisms have been isolated from the circulating blood of the vole. Certain of the features of these organisms may be of sufficient interest to be presented in some detail. Two strains of organisms (9825 and 9827) isolated from two grahamella-infected voles simultaneously with the tested strain (9826) of vole grahamella are culturally identical with the latter and are regarded as grahamella strains. Later on cultures were obtained from the heart's blood of two voles trapped in cold, winter weather and found frozen. Another culture was obtained from the heart's blood of an old vole inoculated long previously with grahamella grown in culture. No grahamellae were demonstrable in post-mortem blood films prepared from the latter three animals at the time of planting of cultures, but this finding is probably of less significance than in case of blood films made during life. All three strains were Gram-negative and non-acid-fast.

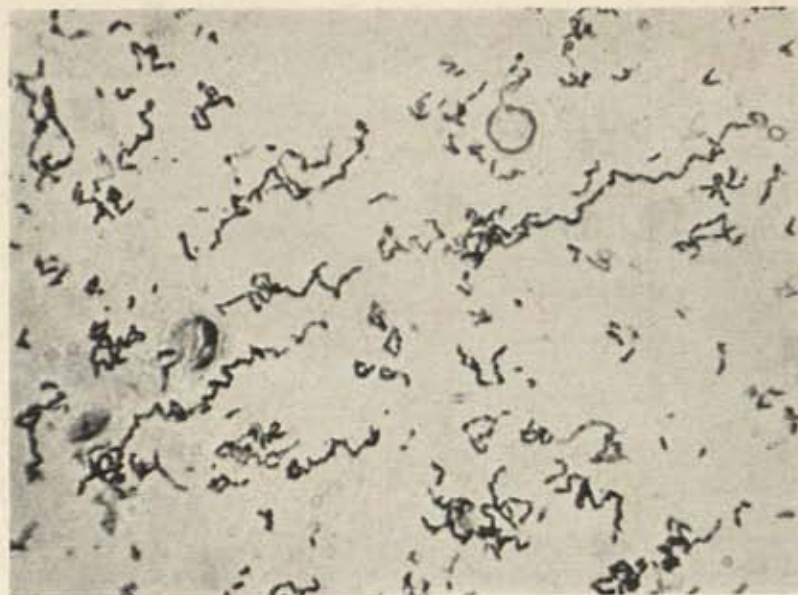


FIG. 13. Chain formation in *Grahamella peromysci* grown in peptone beef bouillon with hemoglobin. Giemsa $\times 1275$.

Strain 9879.—Source, heart's blood of vole taken frozen from trap, Wakefield, February 20, 1941. A growth obtained in leptospira medium appeared as a fine granular cloud at top of medium. The granules were soft and easily spread, not in tough masses as in cultures of the vole grahamella. In subsequent transfers, a whitish cloud forms at the top of leptospira medium, the colonies on blood agar are similar to those of grahamella but tend to coalesce. In peptone beef broth with hemoglobin, growth seen in minute particles on walls of tube—fluid clear; in peptone beef broth with serum, similar but less abundant growth. Microscopically the cultures show an organism growing largely in filaments and forming loose aggregates. Individual rod forms are no longer but average thicker than those of the vole grahamella. Intermingled with the small elements are unevenly stained globules, bluish when lightly stained and often attaining a diameter of four microns. Films from blood agar colonies present rather dense masses, in the interior of which are large amounts of blue-stained amorphous material associated with recognizable organisms. Smaller aggregates consist of organisms intermingled with coarse globules. Non-pathogenic for the white mouse.

Strain 9888.—Source, heart's blood of vole taken dead from trap, Wakefield, March 26, 1941. Growth in leptospira medium in granules near top resembling those of grahamella. On blood agar colonies moist, opalescent, not becoming umbilicated as seen in vole grahamella colonies. In peptone beef broth with hemoglobin there is abundant growth in film on wall of tube, fluid not clouded, and in peptone beef broth

with serum, growth in granules on wall of tube, no clouding—the growth in both fluid media being more abundant and quite unlike that of the proved grahamella culture. In stained films this organism occurs in tortuous beaded filaments showing large laterally-projecting elements suggesting branching. Free globoid or rounded elongate bodies occur in considerable number (Fig. 12). Some take a clear blue stain, others stain unevenly, often with a suggestion of included granules. Such globules occasionally attain the size of a leucocyte. Aggregates occur composed in part of coarse globular elements, in part of recognizable organisms. In films of older cultures there are dense masses of reddish ill-defined elements. This organism is probably slightly pathogenic, one of four white mice, injected subcutaneously and intraperitoneally, dying within four days.

Strain 9812.—Source, heart's blood of an old vole trapped about one year previously. Following splenectomy, September 26, 1940, a severe bartonellosis developed which remained apparent up to December 10, 1940. At no time was grahamella found in blood films. Following the injection of grahamella culture material on December 3, grahamella-infected red cells appeared in the blood on December 17. The animal when killed, April 21, 1941, appeared scrawny, showed defective teeth and swelling near the heel of one hind foot. Leptospira media planted with heart's blood in six days furnished a growth appearing as whitish granules near the top of the medium. Transferred to blood agar slants, growth appeared in small transparent colonies and milky coalesced colonies forming a thick elevated

growth resembling a thick film of paraffin. In fluid peptone beef broth and hemoglobin, a rather heavy sediment and fine particles adherent to wall of tube appear, the fluid remaining clear. Stained films show an organism growing in beaded filaments and compact masses. Great numbers of clear blue bodies, rounded or amoebiform, often attaining the dimensions of red blood corpuscles. Some preparations show aggregates composed largely of globoid bodies. No morbidity followed the subcutaneous and intraperitoneal injection of white mice.

In addition to the foregoing strains of organisms derived from the heart's blood of the vole, an organism which grows in chains or filaments has been isolated on one occasion from the tail blood of one and on another occasion from the heart's blood during life of two Peruvian mice of the species *Phyllotis darwini linatus*, one of which presented a grahamella infection. This organism, which has been already briefly discussed, grows more rapidly than the various cultured strains of grahamella, in leptospira medium producing a surface zone of loose fluffy growth, and on blood agar grows as a film or in distorted drop-like colonies, and produces a flocculent growth in the fluid media. It is Gram-negative, does not form compact aggregates, and is non-pathogenic for white mice. The deeply stained elements within the filament may appear as minute rods and much thicker coccoids, interspersed with bead-like elements which attain relatively great size. The stained elements of the filament are regularly spaced, the unstained interval being nearly equal to the length of the stained portion except in case of the larger elements. The morphology of this organism is strikingly similar to that of the one isolated from Haverhill fever (Parker and Hudson, 1926). Cultures of an organism which has been isolated with great regularity from this species of *Phyllotis* by Dr. Marshall Hertig, working in Peru, have been submitted for examination and agree in every respect with those of the organism just described.

To summarize—the planting of blood from a small series of trapped voles on appropriate media has yielded cultures of non-motile, Gram-negative organisms having a propensity to grow on certain media in beaded filaments and in each strain associated with coarse globoid bodies. Only one of these strains has proved slightly pathogenic for young white mice on intraperitoneal and subcutaneous injection. While there are also certain similarities in the gross appearance of the cultures and those of grahamella, the

discrepancies are such as to indicate that they are distinct from the vole grahamella. Not only is the frequent occurrence of streptobacillus-like organisms in the blood of the vole and the Peruvian mouse of interest, but the strains obtained may prove useful for further comparative studies in determining the group relationships of the vole grahamella. Serological studies should throw light on the question of their antigenic relationships. (*Listerella monocytogenes* has also been isolated from the central nervous system of a vole, obviously abnormal when taken from the trap and later developing paralysis of the hind legs. Identification by Dr. LeRoy Fothergill.)

General Features and Systematic Position of Grahamellae

All strains cultivated are Gram-negative, non-acid-fast and non-motile. They are not well stained by ordinary aniline dyes, individual organisms being scarcely distinguishable after Loeffler staining, but are well stained by the Giemsa method. They grow readily at room temperature of about 20° to 22° C., also at 28° C. and 37.5° C., are aerophilic but will grow to some extent at the bottom of certain fluid media. They grow luxuriantly on solid media containing large amounts of hemoglobin and also in semi-solid media containing serum in which there is a trace of hemoglobin. Such media as nutrient agar or peptone beef broth do not support growth. The survival properties of all strains kept at room temperature are great, cultures of each strain having furnished growth on transfer after several months—*G. peromysci* after more than eleven months. The grahamellae cultivated from three different hosts have all shown under certain conditions some degree of propensity to grow in beaded unbranched filaments or chains and to produce coarse globoid bodies suggestive of forms occurring in *Actinomyces muris*⁴ cultures.

In regard to classification, the possible relationship of organisms of the genera *Grahamella*, *Bartonella*, *Eperythrozoon* and *Anaplasma* have been discussed by various authors, Neitz, Alexander and du Toit, 1934, having suggested the

⁴ *Streptobacillus moniliformis* Levaditi, Nicolau and Poincloux, 1925, is considered by Topley and Wilson, 1936, to be identical with *Haverhillia multififormis* Parker and Hudson, 1926, and with *Streptothrix muris ratti* Schottmüller, 1914, the latter being placed in the genus *Actinomyces* by Lieske, 1921. Topley and Wilson have suggested the binomial *Actinomyces muris*.

family Anaplasmidae, evidently as a zoölogical rather than a botanical group. Since through cultivation *Bartonella bacilliformis* is revealed to be a flagellated bacterium, and as the propagation on dead media of grahamellae from various hosts furnishes conclusive evidence as to their bacterial nature, the question arises as to whether to continue to consider the blood parasites enumerated above in a major group of uncertain systematic position, as previously suggested, or to undertake the introduction of those organisms which have become better known through cultivation into existing systems of classification. The latter alternative is preferred by the author. Although certain mycologists would place the actinomyces with the HYPOMYCETES-FUNGI IMPERFECTI (Dodge, 1935), bacteriologists find reason to include this type of organism in the SCHIZOMYCETES. In undertaking to classify the *Grahamellae*, the bacteriological system will be followed.

It seems clear from the present studies that organisms, heretofore known as grahamellae, show on cultivation characters suggesting close relationship to organisms of the *Actinomyces* (*Streptothrix*) *muris* type in regard to morphology, growth in filaments, associated globoid bodies, affinity for stains and general cultural characters. If Bergey's "Manual of Determinative Bacteriology," 1939, is followed, they should be included in the family ACTINOMYCETACEAE Chester, order ACTINOMYCETALES Buchanan, class SCHIZOMYCETES. Not only should the grahamella type of organism be incorporated into bacteriological taxonomy, but also it would appear important for the genus *Grahamella* to be retained, on account of peculiar features in regard to the favorable effect of hemoglobin on growth, as well as to habitat and peculiar limitation of multiplication in infections.

In case the classification set forth in Bergey's "Manual of Determinative Bacteriology," 1939, is followed, it is suggested that the key be modified in some way such as the following to include the genus *Grahamella*:

KEY TO THE GENERA OF FAMILY
ACTINOMYCETACEAE

- I. Rods or filaments, usually unbranched
 - A. Unbranched, frequently clubbed, human mouth parasites
Genus I. *Leptotrichia*
 - B. Filaments frequently thickened, occasionally branched. Skin parasites of hogs, possibly of man
Genus II. *Erysipelothrix*

- C. Primary growth generally in small mycelia later forming shorter rods and coccoid forms. Mostly soil forms
Genus III. *Proactinomyces*

- D. Slight propensity to grow in unbranched filaments variable; rods and coccoids with indistinct contour commonly cemented together in dense masses; growth favored by hemoglobin; non-motile, aerobic, Gram-negative, with slight affinity for ordinary aniline dyes, well stained by Giemsa; within red blood corpuscles, non-pathogenic
Genus IV. *Grahamella*

Type species—

Grahamella talpae Brumpt, 1911

Red blood corpuscles of European mole, *Talpa europaea*

Species isolated in culture—

Grahamella peromysci, new species

Red blood corpuscles of *Peromyscus leucopus novaboracensis*. Becomes dispersed in semi-solid media, growth in sheets on surface of blood agar

Grahamella peromysci maniculati, new variety

Red blood corpuscles of *Peromyscus maniculatus gracilis*; infective also for *P. leucopus novaboracensis*. Growth in culture luxuriant; forms colonies in fluid media

Grahamella microti pennsylvanici, new variety.
(*Grahamella microti* Lavie 1921)

Red blood corpuscles of *Microtus pennsylvanicus pennsylvanicus*. Tends not to become dispersed in growth in culture, cemented into tough aggregates, on solid media grows in discrete colonies rather than in sheets

It would appear, however, that there is no general agreement among bacteriologists in regard to classification of organisms included in the order ACTINOMYCETALES. The subject has been recently reviewed by Waksman, 1940, who offers a classification with the family PROACTINOMYCETACEAE, including only mycelium-producing organisms with spores formed by segmentation. No discussion is given of *Actinomyces* (*Streptothrix*) *muris* type of organisms; hence it is not known whether they would be included in the family MYCOBACTERIACEAE, which is distinguished by "mycelium, rudimentary or absent." It is obvious that organisms of the grahamella type may not be properly included in either *Mycobacterium* or *Corynebacterium*, the only two genera listed by Waksman in the MYCOBACTERIACEAE. The classification which he proposes is thus not wholly satisfactory in that his

groups are not sufficiently comprehensive as to include many closely related organisms.

It is possible that the application of bacteriological methods in the study of grahamellae may serve to simplify the situation and prove the identity of some of the organisms heretofore recorded as separate species.

III. HAEMOBARTONELLAE OF SMALL MAMMALS

Haemobartonella infections following splenectomy of the common vole, the local deer mouse, the gray-backed deer mouse, the short-tailed shrew and the gray squirrel have been studied. While uniform failure has attended all attempts at cultivation, morphological study has revealed features of interest, which suggest hitherto unsuspected relationships.

*Haemobartonella microti*⁵ Tyzzer and Weinman, 1939, of the Common Vole

This species has been restudied with reference to its culturability and to the question of its distribution in grahamella-like pattern in the red cells during certain phases of infection. Two strains of this organism were available, one from the same locality as the one formerly studied, i.e. Martha's Vineyard, Massachusetts, the other from a locality near Boston. In two passages of the former strain, induced infections were studied in five splenectomized voles and attempts were made to cultivate the haemobartonella, in two at the height of the infection and in one three months after splenectomy. No growth was obtained either on leptospira medium or on blood agar slants. The second strain was transferred to splenectomized white mice, some of which

were injected at the same time with grahamella from cultures. While the grahamella did not become established in these mice, the haemobartonella was carried through six successive passages. *H. microti* occurred in rather large numbers in the blood of infected mice at the height of infection, but only a mild anemia developed and there were no symptoms. In the first transfer the infection did not become apparent in the blood until the elapse of a fortnight, but in subsequent transfers it had become quite heavy by the end of five days, and in some animals lasted for more than four weeks. The morphology of the strain of *H. microti* passaged in mice shows rather less variation than was presented by the strain which served for the original description of *H. microti*. Nevertheless, this strain is quite similar in its staining qualities and in the morphology of the individual organisms to the original strain, while the rafts of organisms extending over the surface of the red cells and the "stringed bow" arrangement which are characteristic of *H. microti* are found on search. Many attempts have been made to cultivate this strain of *H. microti*, but no growths have been obtained.

In our previous study, two splenectomized white mice inoculated with the blood of a trapped vole presented not only typical bartonellae but also on one occasion red cells containing rods having a grahamella-like distribution. Re-examination of the stained films of these two mice leaves no doubt as to the presence of characteristic grahamellae in the red cells. The possibility of a natural grahamella infection in these two animals may be considered, but in the great number of blood examinations made upon the stock of mice used in the course of our investigation, this is the only occasion upon which grahamella has been observed. In the light of the present study, our previous conclusions relative to the ability of this haemobartonella to assume a characteristic grahamella-like distribution require revision. While we have no proof that this may never occur, it now seems probable that the inoculation of the two mice in question with vole blood resulted in a mixed infection of haemobartonella and grahamella, notwithstanding the failure in the present investigation to produce visible grahamella infection in the white mouse. That the vole grahamella is able to survive following its injection into the splenectomized white mouse, when not microscopically demonstrable in the

⁵ Yakimoff (1928) applies the name *Bartonella arvicolae*, without indicating it to be a new species, to an organism or possibly organisms of the European vole, *Arvicola arvalis*, studied by Zuelzer (1927). About the only indication furnished by the latter author that she is dealing with any organism other than the grahamella in the infections which she describes is the statement that in some instances from 80 to 90 per cent of the vole's red blood corpuscles presented bartonella-like inclusions. Her description applies to organisms seen in the blood of non-splenectomized voles, no suggestion is offered as to the possibility of mixed infection, and the vole's blood is reported not to be infective for rats and mice but infective for dogs. Irrespective of the status of *Bartonella arvicolae* as a species, the identity of any organism alluded to in Zuelzer's paper and the haemobartonella described in the local American vole appears to be improbable. In the present study very closely related host species have been found to harbor biologically distinct haemobartonellae.

blood, is evident by its subsequent isolation in culture from such animals in a number of instances, as already considered in detail under *G. microti pennsylvanici*.

Since in our former study (Tyzzer and Weinman, 1939) a culture was obtained which produced infection of the red blood corpuscles on injection into splenectomized mice, the possibility of survival of *H. microti* in a culture in which the growth really represented that of the vole grahamella was considered. In order to test the survival properties of the former, generous samples of the heart's blood of a mouse showing a heavy infection of *H. microti* was distributed into three tubes of leptospira medium which were then kept at room temperature. The bulk of the implanted blood was withdrawn from the tubes after intervals of five, ten, and sixteen days respectively, and that from each tube was injected subcutaneously and intraperitoneally into a splenectomized mouse. No infection resulted in any animal, indicating that the survival properties of the vole haemobartonella at room temperature are notably low.

In contrast to the ease with which the grahamella of the vole is isolated in culture, all attempts to cultivate *H. microti* have failed notwithstanding the implantation of leptospira medium, in which growth was reported in a previous paper, and of many other media with heavily infected bloods. In view of these consistent failures and of the frequent occurrence in the vole's blood not only of grahamella but of other types of organisms that grow readily in leptospira medium, it now appears improbable that the organism grown in our earlier investigation was *H. microti*. The original purpose of the present study, i.e. to clarify certain confusing points in regard to the differentiation of haemobartonella and grahamella infection in the common field vole, has been accomplished. Not only is there a distinct difference between *G. microti pennsylvanici* and *H. microti* in regard to propensity for growth on artificial media, but the propagation of pure infections of these organisms and associated morphological studies have also aided in correcting our earlier misinterpretation of a mixed infection of the two organisms.

Haemobartonella peromysci, new species, of the
Local Deer Mouse, *Peromyscus leucopus*
novaboracensis

Splenectomy performed on twelve trapped deer mice of the local species was followed by haemo-

bartonellosis in six animals. In one of these, infection was delayed for such a long interval after splenectomy that the contraction of the infection in some unknown manner after the operation seems at least possible. In the other animals haemobartonellae appeared in the blood from two to six days and had disappeared after periods of from eleven to thirty-three days after splenectomy. The six animals in which splenectomy was followed by no evidence of natural infection were obviously younger than the other four, although approaching maturity. In these, induced infections appeared in from five to ten days from the time of inoculation, and organisms were microscopically demonstrable in the blood of four for periods ranging from forty-nine to sixty-three days. In one the infection had disappeared before the fourteenth day after inoculation. Temporary diminution and recrudescence occurred in those which presented infections of long duration. In one animal there were three relapses noted. Nine deer mice of this species, born in captivity, developed no infection following splenectomy. Subsequently induced infections in four of these became apparent in from eight to eleven days after inoculation, and ran a similar course to the induced infections in splenectomized trapped animals. The haemobartonellae increased rapidly from the time of their first appearance in the blood, either following splenectomy of an infected animal or the inoculation of a splenectomized clean animal; the infection had become heavy in one instance two days after splenectomy, and in inoculated animals it usually reached its height in nine or ten days. This rapid increase usually terminated in a crisis characterized by the appearance of a severe anemia and the diminution, or even disappearance, of organisms from the blood. In some instances the initial crisis marked the termination of visible infection, but more frequently the organism subsequently became again apparent in numbers increasing until the precipitation of a second blood crisis, this cycle being repeated several times in long infections. Notwithstanding the severity of the anemia produced, the infected deer mice did not appear definitely ill or especially weak, and such deaths as occurred in the series were not attributed to bartonellosis.

The infection of the local deer mouse was transmitted to splenectomized animals of other species, e.g. white rats, white mice, and voles, by the injection of infected blood. Brief infections

were produced in two of four half-grown splenectomized white rats injected. The inoculation of two splenectomized voles resulted in severe infections, one dying twelve days after inoculation. The other became extremely weak, with reticulocytes constituting more than 40 per cent of the red cells at the end of a fortnight, but had recovered by the end of three and a half weeks after inoculation.

The haemobartonella of the local deer mouse was passed from deer mouse to white mouse to deer mouse, and subsequently through seven transfers in white mice, all animals being previously splenectomized. It would appear that inoculation of white mice followed by splenectomy furnishes visible blood infection only if the operation is performed soon after the inoculation. Thus, a splenectomy nine days after inoculation was followed by a rather heavy haemobartonellosis, but a splenectomy performed at the end of sixteen days was followed by no demonstrable infection. The haemobartonellosis induced in splenectomized white mice is commonly severe and occasionally fatal. No attempt has been made to determine the effects of variation of dosage of infective material. In the course of routine inoculations in which blood with large numbers of haemobartonellae is injected, the organisms appear promptly in the blood, frequently within an interval of four days, although on occasion they have made their first appearance as late as thirteen days after inoculation. There is a rapid increase in the number of haemobartonellae, which terminates in a blood crisis with a suddenly developing anemia and diminution or disappearance of organisms. The mice at this time are somnolent, weak, and show extreme pallor of the exposed skin, with staring of the fur. Hemoglobinuria has not been observed and the urine remains pale in color. Fecal pellets are passed in long strings, due to excess of intestinal mucus. Gangrene of a portion of the tail frequently follows the snipping of the tip in obtaining blood for films. The blood is dull-colored and so thin that it is difficult to prepare satisfactory films. Hemoglobin, as estimated by Tallquist's scale, is commonly below 40 per cent normal. The body temperature becomes very low, rectal readings being frequently below 32.5° C. Notwithstanding the severity of the infection, the majority of the mice show improvement within a few days and, though they may pass through several successive crises, eventual recovery supervenes in most cases. Death oc-

curs most frequently in the initial crisis, and in one instance by the ninth day after inoculation, but has occurred as the result of a severe crisis as late as ninety days after inoculation.

Morphology.—*Haemobartonella peromysci*, as compared with *H. microti*, is very delicate, especially as it appears in the blood of its natural host, so that without intense staining it here might very readily be overlooked. It presents certain characteristics which have apparently not been recognized or their significance not fully appreciated in the haemobartonellae of rodents. Interpretations of stages of development are based on the assumptions of growth and multiplication. The organism in its initial growth on the red cell presents filaments, a large proportion of which are branched (Fig. 15 A, B, and C), and which are commonly found radiating from a central granule or from a faintly stained area (Fig. 14 A, B, and D). Frequently a definite, although rudimentary, mycelium is formed. Later the mycelium or filaments are broken up into small elements that may become scattered over the surface of the red cell or concentrated as a colony on a limited area of its surface. The filaments in their early development appear practically homogeneous but later become definitely beaded and show coccoid or rod-like elements which arise within the filament rather than from a clearcut fission. The filaments may be straight or slightly or markedly tortuous, and frequently associated with them are sheets of protoplasmic growth which stain less intensely and which may present a faint reticulum or appear granular. These sheets may appear very early with rudimentary filaments radiating from the periphery, or they may be situated on well-developed filaments or even rods. When situated laterally on filaments, the development of the latter on the border of the sheet would be conceivable, but such sheets also occur frequently as expansions of portions of the filaments. It is difficult to escape from the conviction that there is a high degree of plasticity in the development of this organism. It would seem probable that such sheets may arise from small elements such as rods and coccoids as well as from filaments.

Transfer to foreign hosts serves to accentuate certain morphological features of *H. peromysci*. In the development of *H. peromysci* in its natural host, *Peromyscus leucopus*, ring forms are rare and in many preparations not demonstrable, and this is also true of its development in the white rat (Fig. 14 C) and the vole (Fig. 14 B). In the

common albino mouse, however, ring forms occur in such numbers and so well developed as to suggest a mixed infection (Fig. 14 D and Fig. 15 D).

They may form within filaments or from smaller elements which arise from the latter. With the development of the organism on the red cell, the

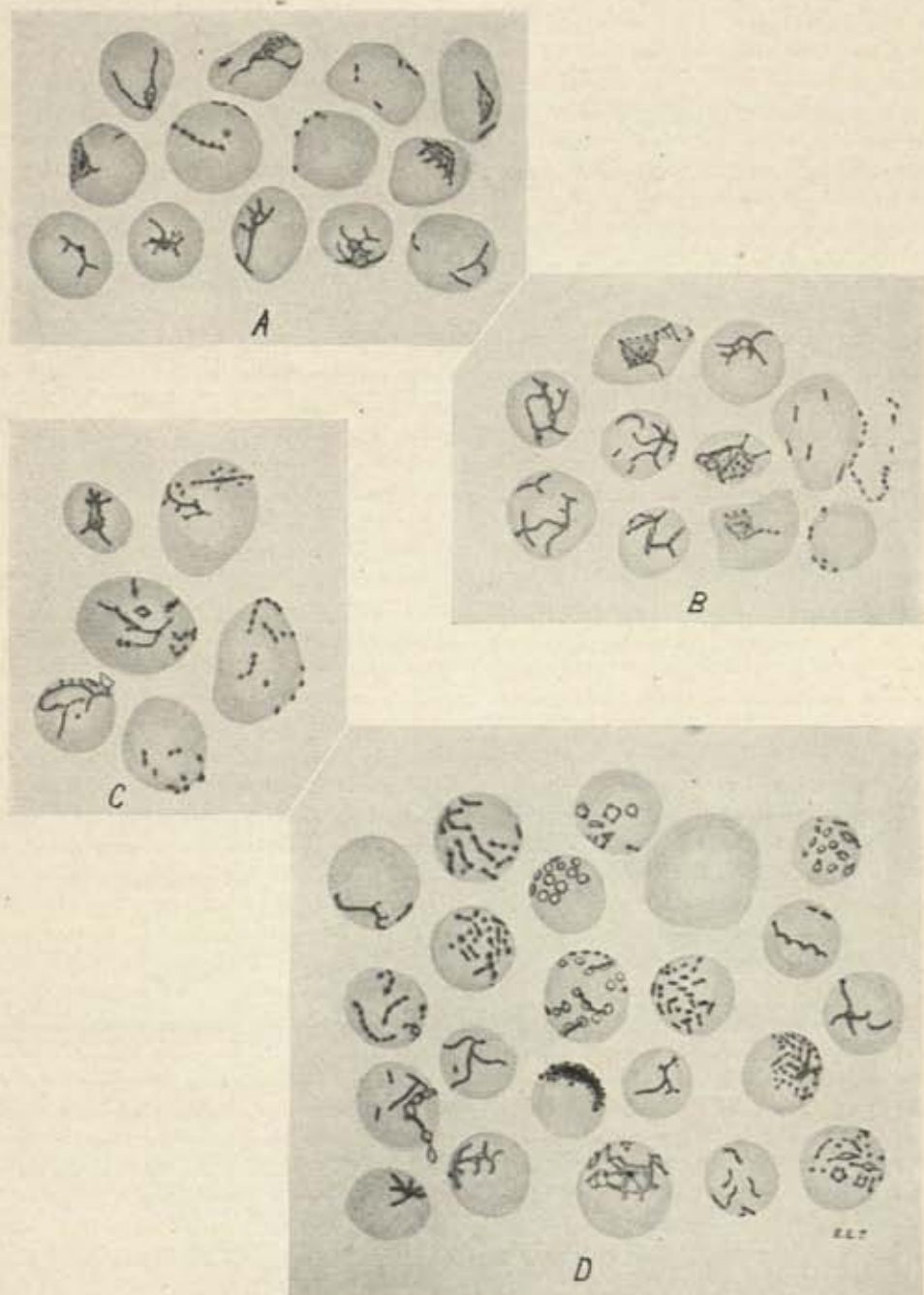


FIG. 14. *Haemobartonella peromysci* of the local deer mouse—selected erythrocytes drawn at 2000 diameters. A. From the blood of the natural host, showing branching forms originating in deeply stained granules, also chains, sheet-like growths and isolated elements. B. The same organism on transfer to the vole. C. Infected erythrocytes from an experimentally infected white rat. D. Morphological modification with excess of coccoids and ring forms on transference to white mouse.

filaments may give rise to a large number of coccoids and rods either of which may become expanded and show indistinct outlines. While the ring forms apparently may arise from any of these elements, the larger rings apparently develop from the indistinct or "blurred" forms,

often appearing uneven with several granules or concentrations of the protoplasm. The significance of the ring forms which constitute such a prominent feature of the infection in the white mouse is not clear, but there is at present no basis for assuming that they represent degeneration

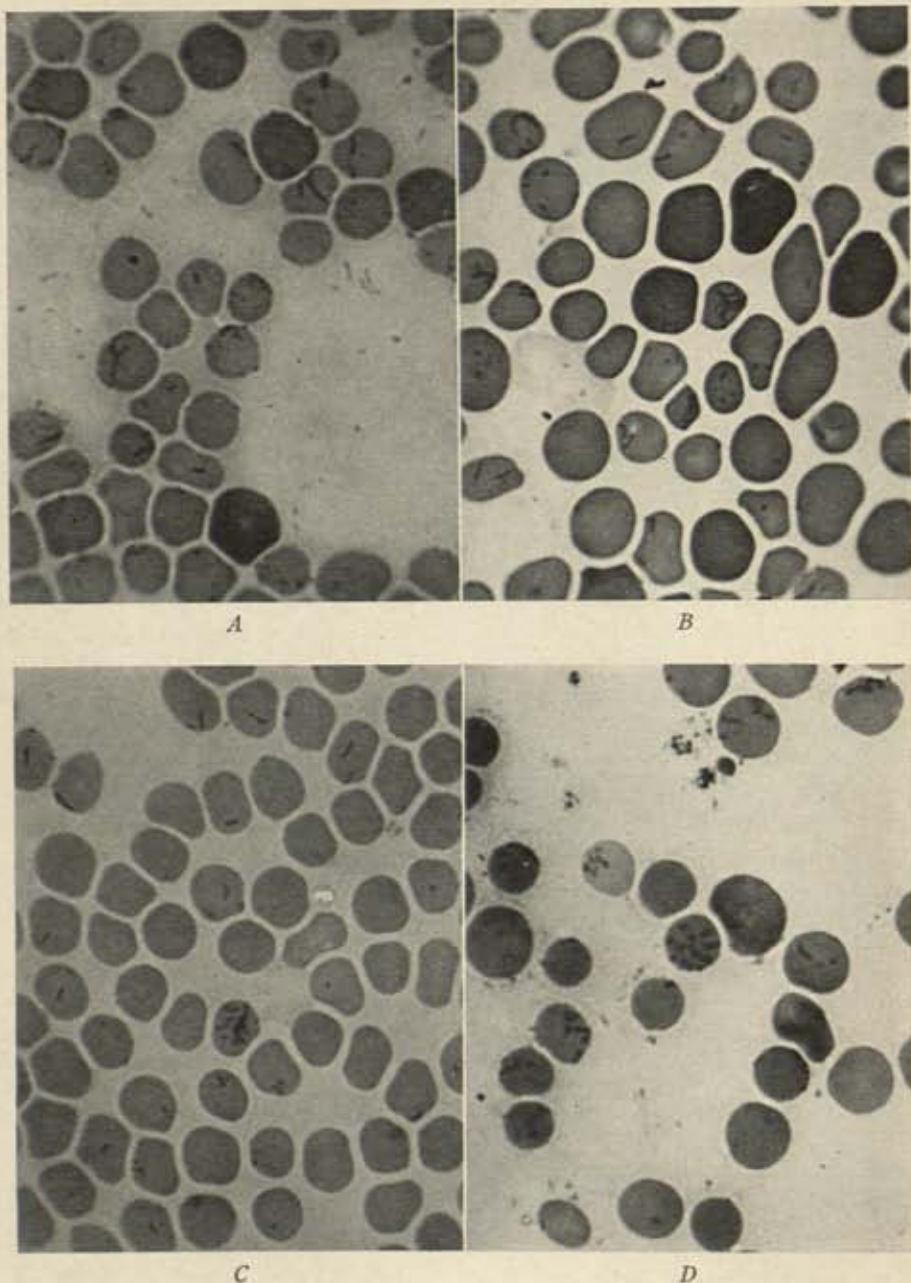


FIG. 15. Giemsa-stained blood films from animals infected with *Haemobartonella peromysci*, taken at 1275 diameters, showing branching forms in A, B and C. A. Natural infection in local deer mouse, 7 days after splenectomy. B. Induced infection in splenectomized vole. C. Induced infection in splenectomized local deer mouse. D. Induced infection splenectomized white mouse—coccoid forms in blood showing severe anemia.

forms. Rods or filaments from which rings are forming become more and more indistinct. Coccoids, rods and rings are rather evenly distributed at intervals, generally over a portion of the surface, less frequently over the entire surface of red cells, but occasionally are accumulated in a dense mass at the margin of the cell. A single cell may show long and short rods and all stages between minute coccoids and coarse rings. The infection in the white mouse also presents markedly tortuous filaments, shorter elements which are sharply bent and also expanded growths with processes anastomosing to form a coarse web. Induced *H. peromysci* infections of the vole present rudimentary mycelia, branching filaments and rods, but few coccoid forms, and ring development is practically negligible. Deeply stained microcytes are often largely covered with organisms. In this animal the number of organisms is maintained at a high level after the development of anemia. The blood of the infected rat presents filaments, many of which branch, while the smaller elements are predominantly coccoid in morphology. Deeply stained microcytes are often heavily infected and may then present an irregular outline.

At the time of the blood crisis, whether of the deer mouse, common white mouse, or vole, there is a change in the shape of the infected red cells which tend to become globular. The lack of uniformity in the diameter of the red cells as seen in dried films is not, however, based wholly upon

change in shape, for the globular erythrocytes seen in fluid blood at this time vary considerably in diameter. In stained blood films considerable numbers of free organisms occur. These have a less distinct outline than those attached to the red cells and in general appear larger, some being obviously distorted. Early in the anemic period when reticulocytes are abundant, the haemobartonellae are not found to any extent on this type of cell but are distributed quite generally on the red-staining erythrocytes. With the development of an extreme anisocytosis, both the large reticulocytes and the intensely staining microcytes are seen with great numbers of attached organisms.

Haemobartonella peromysci maniculati, new variety, of the Gray-backed Deer Mouse, *Peromyscus maniculatus gracilis*

A haemobartonella appeared after splenectomy in three gray-backed deer mice, two of these animals showing a mixed infection with an eperythrozoon, and the third a triple infection with an eperythrozoon and a grahamella present. The time of appearance of the haemobartonellosis showed wide variance, five days after splenectomy in the animal with the triple infection, and forty-one and forty-six days respectively in the other two. It seems probable that the long delay in the development of this infection in the latter two animals is attributable to the incidence of an associated eperythrozoon infection. The effect

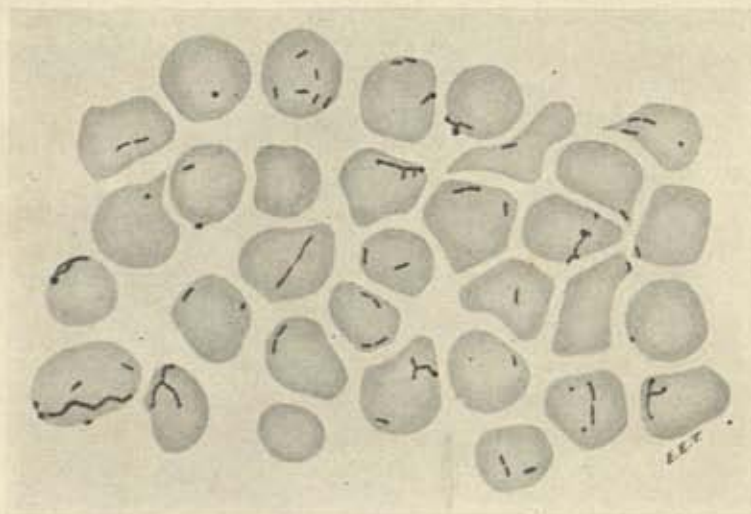


FIG. 16. *Haemobartonella peromysci* (var.) *maniculati* in blood of splenectomized gray-backed mouse. Note filamentous and branching forms. Drawn at 2000 diameters.

of one infection upon another will receive further consideration later on.

The haemobartonellosis, after making its appearance in the gray-backed mice, was followed in two of these animals over a period of five weeks during which severe anemia was noted on various occasions. The infection was passed to a common deer mouse in which it persisted for more than sixty days after inoculation. A small amount of this animal's blood showing great numbers of organisms was injected into two splenectomized white mice without resulting infection. Another splenectomized white mouse which was injected with blood from a gray-backed mouse at the height of its haemobartonellosis also failed to develop visible infection. Hence it appears that the haemobartonella of the gray-backed mouse differs from that of the common deer mouse in that it is relatively non-infective for the splenectomized white mouse.

Notwithstanding the very pronounced biological differences already noted, the morphology of this haemobartonella is so similar to that of the common deer mouse that no distinctive feature has been found for their microscopic differentiation (compare Figs. 14 A and 15 A with Figs. 16 and 17), although the former organism as it occurs in its natural host appears to be in general more slender. Filamentous and branched forms

occur in considerable numbers, the coarser filaments appearing to arise from a rounded granule, and short filaments radiating from a more faintly stained central sheet are occasionally seen. Delicate rods constitute the preponderating form although minute coccoids occur in small numbers. Many of the rods are even more slender than any of the grahamellae of the hosts studied. This organism when transferred to the common deer mouse presents a remarkable morphological transformation. In this species it is comparatively coarse and, although filaments are present, large coccoids occur in great number, sometimes in chains but frequently spaced at regular intervals on the surface of the red blood corpuscle (Fig. 18). A few ring forms such as occur in *H. peromysci* when transferred to the white mouse have been found.

Haemobartonella blarinae, new species, of the Short-tailed Shrew, *Blarina brevicauda*

A trapped shrew was splenectomized at the end of five and a half weeks and survived for a total of two and a half months after capture. Grahamella-infected erythrocytes were found previous to splenectomy. Four days after operation, blood films showed a haemobartonellosis of moderate intensity with some indications of anemia, e.g. marked anisocytosis and large num-

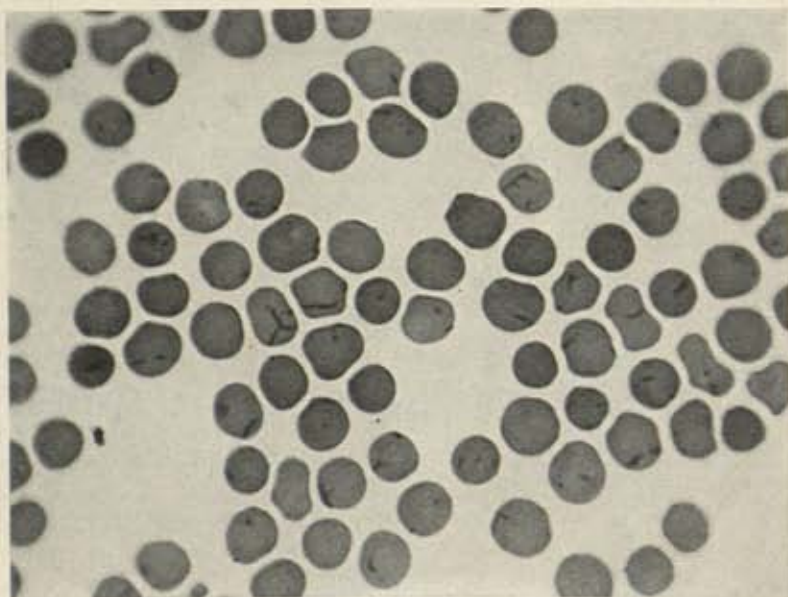


FIG. 17. Branching forms of *H. peromysci maniculati* in blood of gray-backed mouse 41 days after splenectomy. This infection replaced an eperythrozoon infection which followed splenectomy. $\times 1275$.

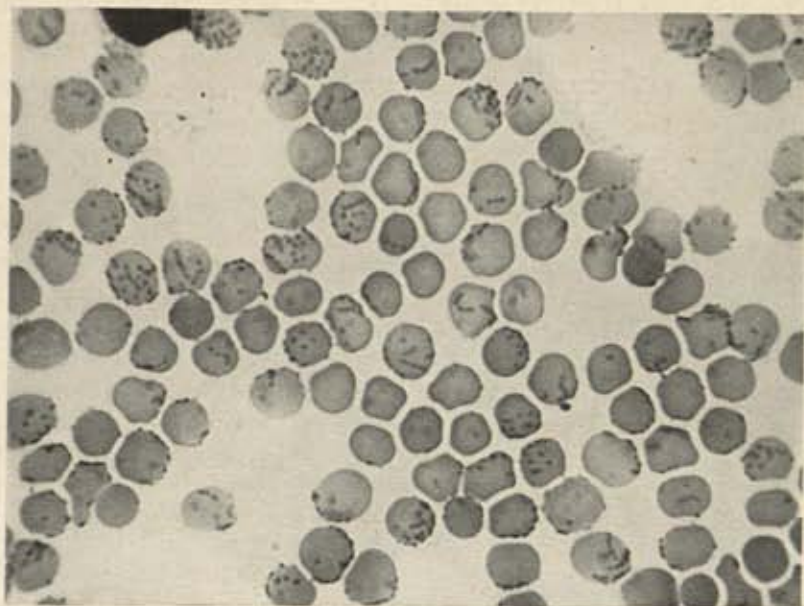


FIG. 18. The same organism as in Fig. 17, 9 days following its transfer to a splenectomized *Peromyscus leucopus novaboracensis*. Note morphological transformation. $\times 1275$.

bers of reticulocytes. Blood planted on various media before as well as after splenectomy furnished a growth which, though not tested by inoculation, probably represents the grahamella. The inoculation of two splenectomized local deer mice with blood taken from this shrew before its splenectomy and of two splenectomized white mice with blood taken at the height of its haemobartonellosis failed to produce infection of any sort.

Another shrew splenectomized four weeks after being taken in a trap also survived for a period of two and a half months. The blood presented haemobartonellae three days after splenectomy, the infection soon became intense, and, although showing some degree of fluctuation, was maintained at a relatively high level until death. No grahamella-infected red cells were found either before or after splenectomy. While there was quite a severe anemia in this animal throughout the course of the infection, the only symptom noted was temporary loss of appetite on two occasions. *Leptospira* medium and blood agar slants planted with splenic tissue at the time of operation and a great variety of media planted with blood twelve days later furnished no growth.

The haemobartonella which appeared in the blood of the above two shrews in three and four days after splenectomy shows in the earlier stages

of infection extreme polymorphism, with delicate rods and coccus-like forms, often occurring in chains but with a large proportion of coarser elements, each with a deeply stained bead-like granule. The blood picture ten days after splenectomy shows a marked change. The infection is now extremely heavy so that the greater proportion of the red cells show thickly distributed organisms, with relatively few of the coarse forms seen earlier. Microcytes are encountered, some completely covered with organisms as to be scarcely recognizable.

On studying the coarse forms conspicuous in the early stages of infection, it is found that they appear as thick bands or filaments stretching across the red cells and quite regularly show a bead or globule, situated either at the end or at some point along the course of the filament (Figs. 19 and 20 A). These thicker filaments usually take a somewhat more bluish tint with the Giemsa stain than the more delicate forms which are a dull slaty violet when not stained intensely. There are, however, all grades intermediate between the coarser and the more delicate organisms. The terminal bead in the coarse forms, when not too intensely stained by the Giemsa method, is distinctly reddish in contrast with the bluer substance of the filament. On further inspection, very short filaments are found evidently

sprouting from reddish globular bodies (Fig. 19, above and to left) which thus seem to be of the nature of spores comparable with certain of those of the higher fungi. The filaments frequently show other granules, there usually being one at the growing tip, but such granules are readily distinguished on the basis of their coloration, at least in the coarser filaments, from the reddish germinative globule. The coarse filaments frequently appear as straight bands extending across the red cell, but may attain such length as to project beyond the margin of the latter or even across an adjacent cell (Fig. 19). Such extension of long forms beyond the cells to which they are attached possibly represents a partial detachment resulting from the dragging of the cells in the preparation of the blood film. The coarse forms are frequently clearly banded or they may appear as a string of coarse beads. Branching occurs, the tips of the branches often being expanded.

The more delicate forms of the organism are best studied in the fully developed infection which presents a bewildering variety of types and distributions. Rods and filaments predominate over rounded forms but, such is the intensity of the infection, all types occur in great numbers. Frequently the organisms are spaced at regular intervals on the surface of the red cell, but often there is a localized growth resulting in a dense colony appearing as an intensely stained cap on

some portion of the cell's surface. Rudimentary mycelia showing branches radiating from a central portion containing a reddish-stained granule are well represented. Filaments, rods, coccoids and granular sheets show a wide range in size and in the manner of their distribution. Filaments and rods are sometimes arranged along parallel lines as though wound about the red cell but are also scattered indiscriminately. Thick smooth rings may develop from the coccoid form, but most ring forms present an uneven contour due to the presence of granular thickenings. Frequently such forms appear quadrangular, triangular or bipolar. In several instances rings were also observed distributed along a filament.

In addition to and among the above forms, more expanded, less intensely stained material is found which may be globular or have an uneven and in some instances an ill-defined contour. This reddish material may occur at the ends of mycelial branches or as expansions in a filament and probably also through the transformation of rods or rounded forms. Its similarity to the spore-like bodies in regard to staining qualities as well as the indication that it is a product of growth and development suggests the possibility that it presents the beginning and end of a growth cycle. Thus an anastomosing mycelium may extend from an aggregate of such reddish material (Fig. 19 to right), or filaments may radiate from a central reddish mass. While a large

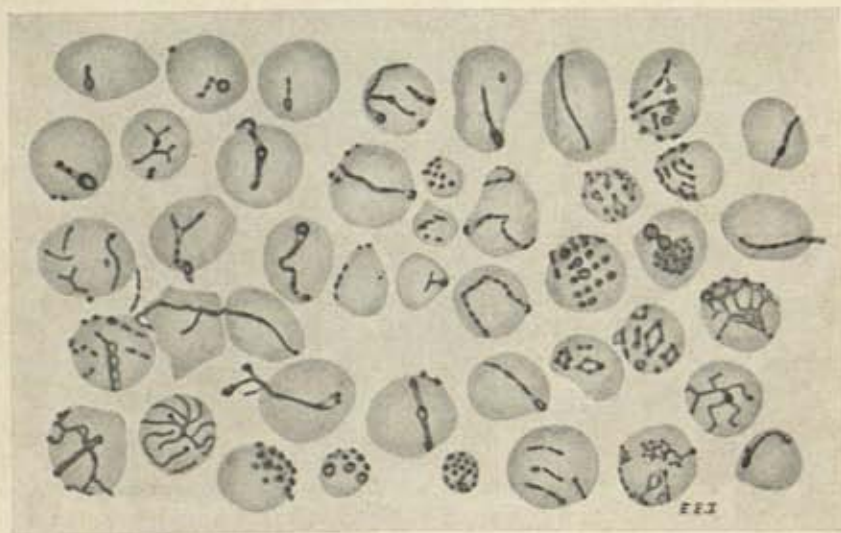


FIG. 19. *Haemobartonella blarinae* of the short-tailed shrew. Selected erythrocytes with various forms of organism. Note coarse filaments, often banded, springing from spore-like bodies, branching and extending beyond the margins of the erythrocyte—drawn at 2000 diameters.

proportion of the simple coarse filaments arise from a well-defined spore-like globule, others arise from an ill-defined reddish mass. This organism, with the luxuriance of its growth in the blood of the shrew and the relatively large size of some of its developmental forms, has furnished additional features indicating the fungus-like character of the haemobartonellae studied.

Haemobartonella sciuri, new species, of the Gray Squirrel, *Sciurus carolinensis leucotis*

A rather light bartonellosis developed in a trapped gray squirrel in ten days after its splenectomy. Four days later the infection had disappeared, was again in evidence after an interval of eight days, but never again became apparent during subsequent observations. The injection of three normal white mice with a suspension of ground splenic tissue produced no demonstrable infection. No attempt was made to transfer the infection to splenectomized mice.

This haemobartonella presents a wide range of variation and assumes rather remarkable forms. Minute rods are of common occurrence and related to these are filaments of various lengths, some continuous, others segmented, often stretching across the face of the red cell and bent over its margin. The rods and filaments vary in

thickness, many in the course of their length being of uneven thickness, and some become very coarse. Within such thickened forms, rounded, often oval bead-like elements develop (Fig. 21). Thus, a filament may be transformed into a beaded chain. The bead-like elements stain a dull reddish at the periphery, but are otherwise faintly stained in contrast to the intensely staining basophilic rods and filaments. Some of the rounded forms have the appearance of large thick rings. Similar beads and rings sometimes arise within rather slender, deeply staining rods, and simulate very closely spores developing within bacilli, but also occur in greatly thickened rods which often stain rather faintly and have a reddish tint. The oval spore-like bodies, with the rod extending lengthwise over its surface, constitute a striking characteristic of the infection. The evidence of the origin of the bead-like and coarse ring forms from rods and filaments is quite conclusive, but their significance is not understood. While they resemble the spore-like forms of the shrew in their staining qualities, no sprouting of filaments from them has been observed. Three beaded filaments radiating from a central granule are shown in Fig. 21, above and to right, and in other instances two divergent filaments are found having a common origin in a single granule.

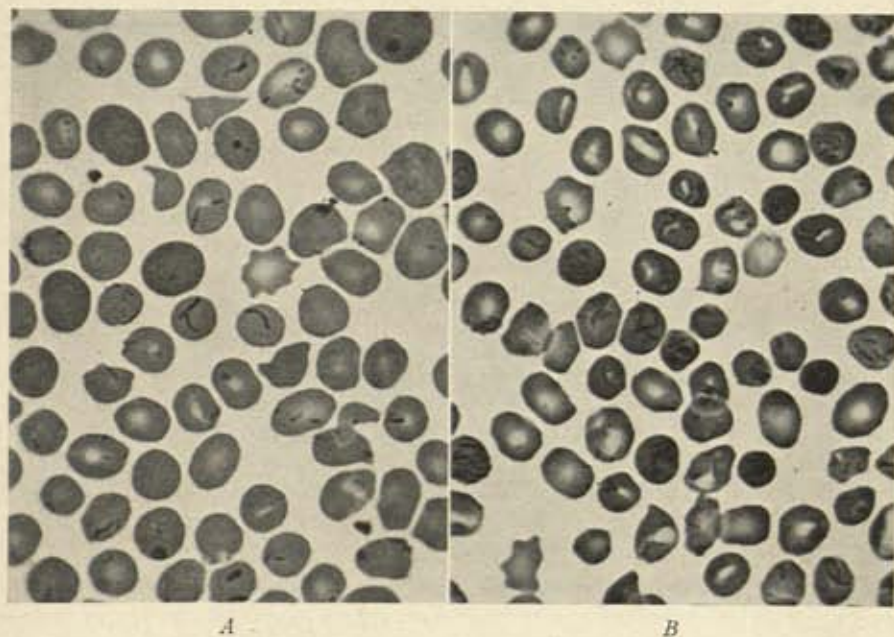


FIG. 20. A. Band forms, *H. blarinae*, in film taken at an early stage of infection in the splenectomized shrew. $\times 1275$. B. Branching forms, later in same infection. $\times 1275$.

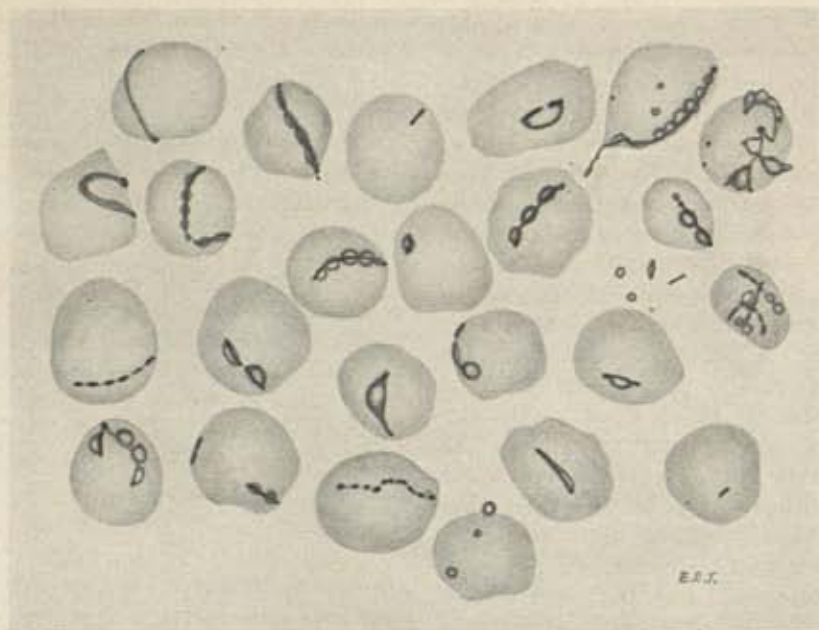


FIG. 21. *Haemobartonella sciuri* of the gray squirrel. Coarse pale-stained beads formed on rods and filaments. Above and to right three filaments radiating from a single granule. $\times 2000$.

Nauck (1927) observed an infection in twelve of a series of twenty *Sciurus vulgaris* splenectomized in Pekin. The organism which he thought might be a bartonella occurred in great numbers in the blood, as rings, rods and comma-shaped forms of variable size, nearly all the red cells being infected. Inoculation of uninfected splenectomized squirrels was successful but the white rat proved refractory.

Indications as to the Systematic Position of Haemobartonellae

Certain well-known characteristics of haemobartonellae, such as their prevalence in a latent condition in various species of animals, their rapid increase following splenectomy attended with the development of severe and often fatal anemia, and the eradication of infection by arsphenamine therapy, have already been discussed. This type of organism differs from *Bartonella bacilliformis* of the human being in that no multiplication in any tissue apart from the blood is known to occur, there are no eruptions associated with infection, and survival outside the body is of brief duration. The present study has served to emphasize the difficulty of cultivation, no success having attended numerous at-

tempts utilizing media upon which *B. bacilliformis* and grahamellae are readily grown.

The chief contribution, however, has been derived from comparative morphological studies of the haemobartonellae of various animals. The haemobartonellae of the two species of deer mice studied and that of the short-tailed shrew all show definite branching in their growth on the surface of the red blood corpuscles, and also evidence of sprouting from a spore-like granule. There is a suggestion of septa in the coarser filaments but multiplication is accomplished largely by the formation of bead-like elements within the substance of the filament. The haemobartonella of the common gray squirrel presents huge, pale-red, spore-like bodies originating in rods and filaments, and may show several filaments radiating from a single granule, but no branching has been observed. Doubtless a more extended study of this organism would reveal additional features. No branching has been observed in *H. microti* although thick fungus-like filaments occur in both vole and mouse blood. In the vole there are short thick forms with a terminal globule suggestive of sprouting from a spore.

For comparative purposes preparations of *H. canis* and *H. muris* also have been studied. In the single film available, the former organism

presents moderate numbers of branching filaments and numerous reddish globules and rings. *H. muris* is represented chiefly by minute elements with no notable tendency to form filaments and hence shows no branching. There are occasional coarse forms with a terminal bead. This organism, the type species of the genus, while presenting the other characteristics of the group, lacks those morphological peculiarities which in certain haemobartonellae furnish a clue as to their systematic position. From the descriptions here furnished it will be obvious that various species found in small mammals present features characteristic of higher fungi, such as the development of branched filaments from spore-like granules and even the formation of a rudimentary mycelium. Doubtless the successful cultivation of haemobartonellae would yield additional information as to their nature. Notwithstanding the indications of relationship with the higher fungi, it is probably well to defer the further classification of the haemobartonellae until the possibilities of cultivation are given further consideration. Thus, from a comparison of the haemobartonellae of small rodents and *Bartonella bacilliformis*, evidence is obtained of a phaenotypic rather than a phylogenetic relationship.

IV. EPERYTHROZOA OF SMALL MAMMALS

Eperythrozoon of the Common Mouse and of the Local Vole

Eperythrozoon coccoides Schilling, 1928, of the common mouse occurs with great frequency in healthy laboratory stock mice, its presence being made manifest by splenectomy. The peculiar property of this organism in preventing or modifying certain haemobartonella infections will be discussed later. This organism is only slightly infective for splenectomized voles, one very light and one moderate but transient infection following the injection of four voles with heavily infected mouse blood. An eperythrozoon of the local vole, probably of the species *E. dispar* described in the European vole, *Arvicola arvalis*, by Bruynoghe and Vassiliadis, 1929, on the other hand, appears from past experiments not to be transferable to splenectomized white mice (Tyzzer and Weinman, 1939). This species as compared with that of the common laboratory mouse presents a relatively large proportion of coccoid forms and few rings. No natural eperythrozoon infection has been observed in fourteen of the local species of deer mice splenec-

tomized, but three gray-backed deer mice from Ossipee, New Hampshire, all showed eperythrozoon after splenectomy.

Eperythrozoon varians, new species, of the Gray-backed Deer Mouse, *Peromyscus maniculatus gracilis*

This species shows a greater variety of forms than either *E. coccoides* or *E. dispar*. At the height of the infection organisms occur in great numbers in the plasma, relatively few being attached to the erythrocytes (Fig. 23). At this time, there are rings, coccoids of various sizes, some of the latter being extremely minute. It appears probable that the minute coccoids may develop into rings and also that the elongate, diplococcoid forms and tetrads may have to do with multiplication (Fig. 22). Slender, faintly staining bacillary forms also occur in the plasma and are also seen attached by one end to the margins of the red cells from which they extend usually nearly vertically (Fig. 24). Wherever an organism comes in contact with the surface of a red cell, it stains intensely. Thus, rods having one end in contact with a red cell present an intensely stained terminal granule, while organisms lying flat against the margin of the red cell are stained intensely throughout, or on one side.

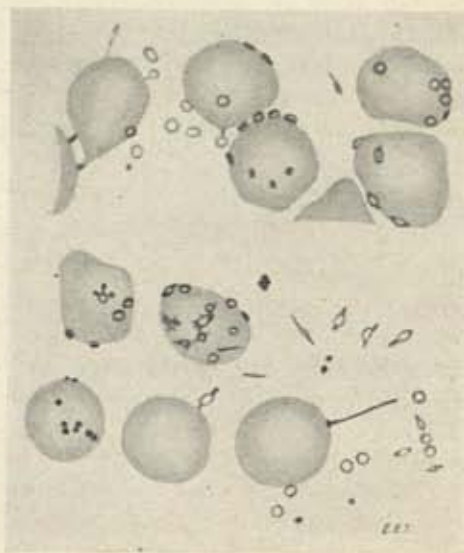


FIG. 22. *Eperythrozoon varians* of gray-backed mouse. Above an area of blood film showing intense staining of organisms where they are in contact with erythrocytes. Below selected cells and organisms showing variability in size and outline. Small coccoid forms in pairs or tetrads are probably multiplication forms. $\times 2000$.

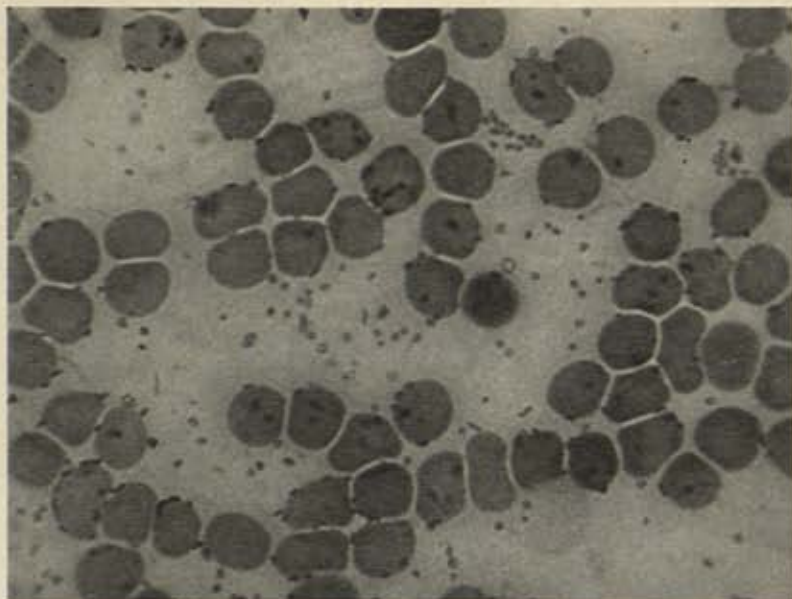


FIG. 23. *Eperythrozoon varians* of gray-backed mouse in blood of splenectomized local deer mouse, 9 days after inoculation. Note elongate forms as well as rings. $\times 1275$.

Many of the bacilliform elements show an unstained lens-like swelling, indicating the formation of a ring within the substance of the rod. Pulled-out, elongate forms of uneven thickness and occasional organisms having an angular process at the side are seen. Pairs and chains of lens-like, coccoid and pulled-out forms occur, which may be explained on the basis of adventitious grouping and distortion. The occurrence at the end of the film of small, amorphous elements corresponding in distribution and size to the well-defined eperythrozoa which they replace is obviously due to some artifact in preparation. It would appear that the physical properties of this organism are such that distortion forms are much more readily produced than is the case in the haemobartonellae studied.

This eperythrozoön appeared following splenectomy in three gray-backed deer mice, in one in mixed infection with haemobartonella and grahamella, in the other two in association with latent haemobartonella alone. In the latter two animals, the eperythrozoön had not appeared eleven days after splenectomy, but was present in heavy infections by the twentieth day, which thereafter gradually diminished in intensity and were replaced by the end of forty-one and forty-six days respectively by haemobartonella in-

fections. The eperythrozoön infections were associated with a notable degree of anemia, as indicated by an increase in reticulocytes, but not approaching in severity that developing in the haemobartonellosis which followed. Attempts made at the height of the infection to cultivate the eperythrozoön on various media failed. • A small amount of blood from the animal showing triple infection was injected into a splenectomized white mouse without result, but the inoculation of a splenectomized local deer mouse was followed by a haemobartonella infection soon replaced by an eperythrozoön infection. While both organisms were present in the blood of this animal, an attempt was made to passage the infections to two splenectomized white mice and from one of these to a third splenectomized mouse, but in none of the three animals did either type of organism make its appearance. Blood taken at the height of the eperythrozoön infection in one of the gray-backed deer mice was injected into a splenectomized local deer mouse, producing an extremely heavy eperythrozoön infection not followed by haemobartonellosis (Figs. 23 and 24). Thus, it is clear that this eperythrozoön is readily transferred to another species of deer mouse. Failure even in the few attempts to pass it to splenectomized white mice furnishes rather conclusive evidence that the eperythro-

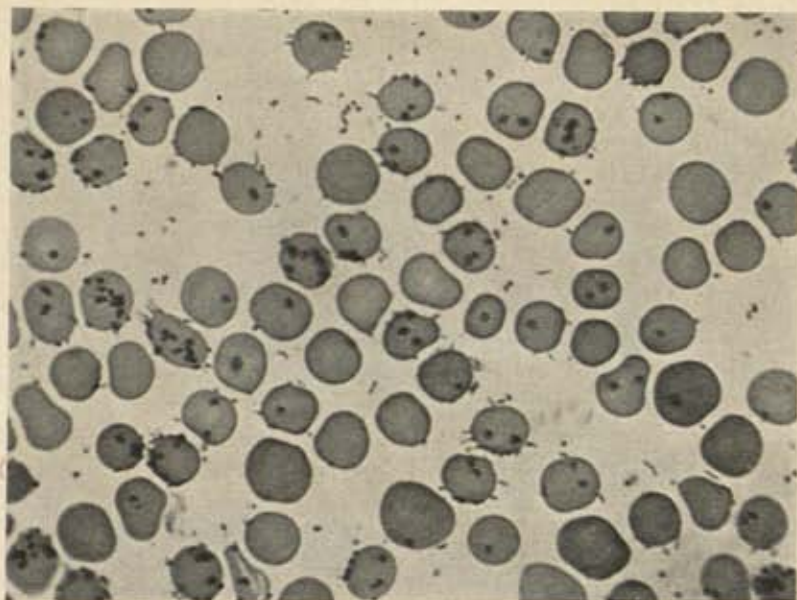


FIG. 24. Blood of same animal 21 days after inoculation, showing small coccidia and elongate forms extending vertically from the surface of the erythrocyte. $\times 1275$.

zoön of the gray-backed deer mouse is distinct from *E. coccoides*.

V. GENERAL CONSIDERATIONS

Purity of Infections and Cultures

The purity of given infections is ever open to question, especially in case of those of the types under discussion which are quite frequently associated with one another in the same animal. The occurrence of mixed infections of haemobartonella and eperythrozoon is so frequent in nature that the possibility also of mixed infections of different species of haemobartonella may not be wholly disregarded. It would be ideal to produce infections by the injection of single organisms, but even if it were possible to accomplish this, the technical difficulties in isolating single organisms either within or attached to erythrocytes, appear to be very great. Isolation in culture should go far in the identification of various infections of the types studied. While the grahamellae of various species of animal have been found to grow readily on certain media, their cultural characteristics should be made the subject of further study. The readiness with which organisms of this type develop in leptospira medium planted with infected blood sets them off quite sharply from the haemobartonellae and the eperythrozoea. In the present pre-

liminary study, rather definite differences have been noted in the gross cultural characteristics of grahamellae derived from different hosts. The morphological variation of the cultivated organisms is so extreme as to raise the question as to purity of the culture strains. The variation in the type of colony associated with slight differences in the media or in the inoculum is also a matter of interest. Culture strains derived from various types of colonies picked from blood agar slants appear in all respects identical and the conclusion is reached that we are dealing with pure rather than mixed cultures. Pure line cultures derived from single organisms would, however, present certain advantages. Less exact methods for eliminating certain organisms from mixed infections, such as repeated passage in a foreign host for the elimination of grahamella or arsphenamine treatment of the infected animal for the elimination of haemobartonella and eperythrozoon, are useful if properly checked.

The possibility of the occurrence of organisms of the "L" or so-called "pleuropneumonia type" in the animals employed or even in the cultures derived from them is by no means eliminated. While the laboratory-reared stock utilized has never shown any indication of disease, swellings of the feet and inflammation around the molar teeth have been observed in trapped voles kept

over long periods. Since the status of the "L" type organisms appears not to be definitely established, and since their study requires an entirely different approach with the employment of special media and techniques, it has not as yet been undertaken.

Host Specificity of Grahamellae, Haemobartonellae and Eperythrozoon

The results obtained in attempts to transfer grahamella infections to host species other than the ones in which they have been found demonstrates that this may be accomplished in closely related animals such as the two species of deer mice employed (Table 3, Nos. 9797 and 9800), and also occasionally with species that seem quite distant from one another, as the vole and the common white mouse. In two instances the inoculation of vole's blood showing both haemobartonella and grahamella into splenectomized white mice has produced mixed infections with grahamella, in which, however, grahamellae were apparent only on one occasion. *Grahamella pennsylvanici* may also survive in animals in which it is not microscopically demonstrable. Thus, in recent experiments, it has been recovered in culture after a sojourn of five weeks in splenectomized mice, in none of which were infected red cells found at any time.

Data relating to attempts to infect various species of animals other than the natural host are presented in Table 2.

The series of animals inoculated with the grahamellae of other host species are obviously too small to furnish more than suggestive results when certain factors involved in the experimental procedure are taken into account. The intracorporeal situation of the organisms, as well as their being introduced into the test animals within corpuscles of a foreign species, may have a bearing on the success of the inoculation. It would seem that the probability of organisms contained within cells of a foreign host being destroyed by phagocytosis should be greater than would be the case with similar organisms free of such cells. Furthermore, the injection of blood containing infected red cells is not invariably successful for the transmission of infection to susceptible animals of the same species. The injection of grahamellae from newly isolated cultures would probably constitute a more reliable test and too few animals have been injected with cultured grahamellae from other species to estab-

lish host specificity as a wholly reliable basis for differentiating species of grahamellae. The distinctive characters observed in grahamella of various host species when propagated in culture media offer more conclusive evidence as to the multiplicity of grahamella species.

Certain of the haemobartonellae are readily transferred to splenectomized animals of species other than those in which they occur naturally. Some species are uniformly susceptible, e.g. the white mouse to *H. microti* of the vole and to *H. peromysci* of the local deer mouse. The splenectomized white rat appears non-susceptible to the former and slightly susceptible to the latter organism, presenting transient infection in a certain proportion of young splenectomized animals. Haemobartonellae that are morphologically indistinguishable, such as those of the two species of deer mice studied, show definite biological differences, one being non-infective for splenectomized white mice, the other being uniformly infective and pathogenic. Profound modifications in morphology have attended their transference to certain foreign hosts. Such changes have been observed in *H. microti* and *H. peromysci* when transferred to the common albino mouse and in *H. peromysci* var. *maniculati* transferred to *Peromyscus leucopus novaboracensis*.

In case of eperythrozoon infections, *E. coccoides* of the common mouse may produce transient infection in splenectomized voles, as shown in recent experiments, but the *E. dispar* of the vole has not infected splenectomized white mice (Tyzzar and Weinman, 1939). The eperythrozoon, *E. varians*, of the gray-backed deer mouse is readily transferred to the local deer mouse but not to the splenectomized white mouse. It would appear that infectivity for various host species should prove to be of value in the differentiation of species or varieties of the latter two types of organism under consideration.

Interference Phenomenon in Associated Infections

During the study of the infections above described, it was noted that the haemobartonellosis induced in the splenectomized white mouse by inoculation with *H. peromysci* of the local deer mouse, was made latent for long periods by pre-existent eperythrozoon infection in the inoculated animal. Furthermore, if white mice which were already infected with the haemobartonella in question were inoculated with *E. coccoides*, the former organism promptly disappeared from

TABLE 2
SUSCEPTIBILITY, AFTER SPLENECTOMY, OF OTHER THAN NATURAL HOST SPECIES TO VARIOUS GRAHAMELLAE, HAEMOBARTONELLAE AND EPERYTHROZOA*

Type of Organism	Inoculum**	Host of Origin†	Species Inoculated	Inoculated	Number Infected	Remarks
Grahamella	Blood	<i>M. pennsylvanicus pennsylvanicus</i>	White Swiss mouse	5	2	Grahamella had disappeared from donor's blood. One animal half-grown; the other mature. Grahamella isolated in culture from blood of one. These not splenectomized.
Grahamella	Blood	<i>M. pennsylvanicus pennsylvanicus</i>	White Swiss mouse	7	0	
Grahamella	Blood	<i>M. pennsylvanicus pennsylvanicus</i>	White rat (Wistar)	2	0	
Grahamella	Culture	<i>M. pennsylvanicus pennsylvanicus</i>	White Swiss mouse	8	0	
Grahamella	Culture	<i>M. pennsylvanicus pennsylvanicus</i>	Ibid., nursing	8	0	Grahamella latent or very rare in dog. Recipients not laboratory-reared.
Grahamella	Culture	<i>M. pennsylvanicus pennsylvanicus</i>	<i>P. leucopus novaboracensis</i>	1	0	
Grahamella	Blood	<i>P. leucopus novaboracensis</i>	White Swiss mouse	10	0	
Grahamella	Blood	<i>P. leucopus novaboracensis</i>	White Swiss mouse	8	0	
Grahamella	Blood	<i>P. leucopus novaboracensis</i>	<i>Phyllotis darwini linatus</i>	2	1?	Grahamella latent or very rare in dog. Recipients not laboratory-reared.
Grahamella	Culture	<i>P. leucopus novaboracensis</i>	White Swiss mouse	1	0	
Grahamella	Culture	<i>P. leucopus novaboracensis</i>	<i>Macaca mulatta</i>	1	0	
Grahamella	Blood	<i>P. maniculatus gracilis</i>	White Swiss mouse	1	0	
Grahamella	Blood	<i>P. maniculatus gracilis</i>	<i>P. leucopus novaboracensis</i>	1	0	Failure to infect one entire group of 3 indicative of non-infective inoculum. One not splenectomized.
Grahamella	Culture	<i>P. maniculatus gracilis</i>	<i>P. leucopus novaboracensis</i>	3	3	
Grahamella	Blood	<i>Blarina brevicauda</i>	White Swiss mouse	2	0	
Grahamella	Blood	<i>Blarina brevicauda</i>	<i>P. leucopus novaboracensis</i>	2	0	
Grahamella	Blood	<i>Pitymys pinetorum</i>	White Swiss mouse	1	0	The blood of one of 5 animals not showing infection was examined only once, one had received arsphenamine before inoculation, and 3 were injected with non-infective blood. Light transient infections. Severe infections, one fatal.
Grahamella	Blood	<i>Phyllotis darwini linatus</i>	White Swiss mouse	5	0	
Grahamella	Blood	<i>M. pennsylvanicus pennsylvanicus</i>	White Swiss mouse	27	23‡	
Grahamella	Blood	<i>M. pennsylvanicus pennsylvanicus</i>	<i>P. leucopus novaboracensis</i>	8	0	
Haemobartonella	Blood	<i>M. pennsylvanicus pennsylvanicus</i>	<i>P. eremicus</i>	1	0	The blood of one of 5 animals not showing infection was examined only once, one had received arsphenamine before inoculation, and 3 were injected with non-infective blood. Light transient infections. Severe infections, one fatal.
Haemobartonella	Blood	<i>M. pennsylvanicus pennsylvanicus</i>	White rat	7	0	
Haemobartonella	Blood	<i>M. pennsylvanicus pennsylvanicus</i>	Dog	2	0	
Haemobartonella	Blood	<i>P. leucopus novaboracensis</i>	White Swiss mouse	40	35‡	
Haemobartonella	Blood	<i>P. leucopus novaboracensis</i>	White rat (Wistar)	4	2	One injected with blood showing E with H latent failed to develop bartonellosis.
Haemobartonella	Blood	<i>P. leucopus novaboracensis</i>	<i>M. pennsylvanicus pennsylvanicus</i>	2	2	
Haemobartonella	Blood	<i>P. maniculatus gracilis</i>	White Swiss mouse	3	0	
Haemobartonella	Blood	<i>P. maniculatus gracilis</i>	<i>P. leucopus novaboracensis</i>	2	1	
Haemobartonella	Blood	<i>Blarina brevicauda</i>	White Swiss mouse	2	0	One light, one heavy, transient infection. Both infections intense.
Haemobartonella	Blood	<i>Blarina brevicauda</i>	<i>P. leucopus novaboracensis</i>	2	0	
Haemobartonella	Blood	<i>M. pennsylvanicus pennsylvanicus</i>	White Swiss mouse	5	0	
Haemobartonella	Blood	<i>P. maniculatus gracilis</i>	<i>M. pennsylvanicus pennsylvanicus</i>	4	2	
Haemobartonella	Blood	<i>P. maniculatus gracilis</i>	White Swiss mouse	3	0	Both infections intense.
Haemobartonella	Blood	<i>P. maniculatus gracilis</i>	<i>P. leucopus novaboracensis</i>	2	2	
Haemobartonella	Blood	<i>P. maniculatus gracilis</i>	<i>P. leucopus novaboracensis</i>	2	2	
Haemobartonella	Blood	<i>P. maniculatus gracilis</i>	<i>P. leucopus novaboracensis</i>	2	2	

* Animals tested for susceptibility in former investigation (Tyzzer and Weinman) included.

** The organism in question, demonstrated microscopically in the blood employed, unless otherwise stated, in most cases alone but in others with one or both the other types of organism apparent or latent in the donor. E = eperythrozoon; H = haemobartonella.

† *M.* = *Microtus*; *P.* = *Peromyscus*.

‡ Passages in white mice included.

TABLE 3
THE COURSE OF NATURAL MIXED GRAHAMELLA, HAEMOBARTONELLA AND EPERYTHROZOON INFECTIONS IN THE GRAY-BACKED DEER MOUSE FOLLOWING SPLENECTOMY AND OF THE SAME INFECTIONS INDUCED IN THE LOCAL SPECIES OF DEER MOUSE

Animal	Splenec- tomy	Inoculation	October										November							December					
			8	9	10	11	14	15	18	21	24	28	30	2	4	7	14	19	30	7	14	18	19	23	31
Gray-backed deer mouse*				0				0			E	E	E		E	E	H	H	H	H	0	HE		GE	
9817	Oct. 4	Grahamella culture Dec. 9		HEG	HEG	EHG	HG	HG	GH	G	HG†														
9818	Oct. 4	None		0							E	E	E			E	E	H	H	H	0	H		HG	
9819	Oct. 4	Grahamella culture Dec. 9		0							E	E	E												
Local deer mouse**																									
9797	Sept. 19	Blood from 9818 Oct. 24 Grahamella	0				0			0		0	H	H	HE		EH	0	H	H	0	0		GH	
9800	Sept. 19	Blood from 9819 Oct. 24 Grahamella	0				0			0		0	E	E	E		E	E	0	0	0	G		G	
9857	None	culture Dec. 9 Grahamella culture Dec. 9																					0	0	G

* *Peromyscus maniculatus gracilis*.

** *Peromyscus leucopus novboracensis*.

† Death.
H haemobartonellosis.
E eperythrozoon infection.
G grahamella infection.
In mixed infection the sequence of the letters indicates the relative preponderance of organisms, the heavier preceding lighter infection.

the blood. This example of "interference" or suppression of one infection by another has received consideration in a separate paper (Tyzzer, 1941). While the haemobartonella in the presence of *E. coccoides* may disappear from the blood, as far as may be determined by microscopic examination, it is by no means wholly eradicated, and following the gradual decrease in the number of eperythrozoon to near the vanishing point, a full-blown haemobartonellosis may suddenly appear weeks or months after inoculation. The eperythrozoon has thus in no way rendered the splenectomized white mouse immune to the haemobartonella. There is a point to be noted in the alternation of these two infections. Although well-established *H. peromysci* infections are promptly suppressed by infecting the animal with *E. coccoides*, it is only after infections of the latter organism have run their natural course and have nearly or actually disappeared that the latent haemobartonella reappears. Thus, the haemobartonella has no pronounced suppressive effect upon the eperythrozoon. In this instance an organism occurring in its natural host interferes with induced infections of an organism from another host species, and may thus wholly prevent the severe anemia and its associated symptoms that result from uncomplicated haemobartonellosis.

The association of eperythrozoon and haemobartonella in the gray-backed mouse has afforded an opportunity to follow the course of double infections in their natural host following splenectomy. Data relating to these animals are presented in Table 3. Unfortunately, one animal, No. 9818, presenting triple infection with grahamella, haemobartonella and eperythrozoon was killed accidentally. In this animal for three successive days the three organisms were well represented in stained blood films, but the eperythrozoon was not apparent for ten days prior to the animal's death. In the other two animals eperythrozoon infection ran a course of at least fourteen and twenty-one days respectively before being replaced by haemobartonella.

Thus, with two infections in the natural host, there seems to be some degree of interference, with the eperythrozoon repressing the haemobartonella, although in the case of the triple infection, mixed infection persisted for several days with eperythrozoon being the first to disappear. To what extent the rather heavy grahamella infection present in this case influenced the other two infections is problematical. In animals in

which any one of the three types of infection has run its course and disappeared microscopically from the blood, no immunity to either of the other types of organism has been noted. The inoculation of an animal of another species, i.e. the local deer mouse, with the blood from the triple infection resulted in haemobartonellosis followed by mixed haemobartonella and eperythrozoon infection, with the eperythrozoon being the first to disappear. Thus, *E. varians* on injection together with *H. peromysci maniculati* into a foreign host, e.g. the local deer mouse, has shown no suppressive effect on the latter organism. Another animal of the same species inoculated with the blood of one of the gray-backed mice at a time when it showed only eperythrozoon, the haemobartonella being latent, developed only eperythrozoon infection. Likewise the eperythrozoon of the white mouse, when transferred to a foreign host, i.e. the vole, failed to show any effect upon subsequently induced *Haemobartonella microti* infection. One of four splenectomized voles which were inoculated with *Eperythrozoon coccoides* developed a lasting infection, and another a transient infection. Following the inoculation of all four voles fifteen days later with the vole haemobartonella, a heavy bartonellosis developed promptly in both eperythrozoon-infected voles.

In contrast to the interference effects in connection with associated infections observed in the present study, Neitz (1939) reports that infections with *Babesia canis*, *Babesia gibsoni* and *Rickettsia canis* have an activating effect on latent *Bartonella canis* infection in the dog.

It is possible that the phenomenon of bacterial antagonism found by various investigators (Dubos, 1939—Krasilnikov and Koreniako, 1939—Ark and Hunt, 1941) to be effective in cultures of various organisms may be related in some way to the interference phenomenon observed in mixed infections.

Comparison of Biological Characteristics of Grahamellae, Haemobartonellae and Eperythrozoon

Grahamellae.—In the cultivation of grahamellae from various species of animals on dead media, it is found that they differ appreciably from one another in their growth characteristics. On account of the inability of organisms of this type to multiply on ordinary media and their ready growth in media of high hemoglobin con-

tent, it is difficult to conceive of their multiplying in nature apart from host or vector, although their survival properties in the media in which they have grown is great, e.g. a culture of *G. peromysci* remaining alive for more than eleven months at room temperatures. The fact that the circulating blood is the habitat of grahamellae suggests that some blood-sucking arthropod may serve as vector. The consistent lack of motility of grahamellae under cultivation and the absence of spirals, interpreted as detached flagella, set them apart from *Bartonella bacilliformis* of the human being. It now seems clear that the organisms heretofore recognized as characteristic grahamellae should be regarded as bacteria. Furthermore, on account of the peculiar type of infection produced in mammals, characterized by greatly restricted multiplication and situation within erythrocytes, it seems important that the genus *Grahamella* be retained. As to species of grahamellae, in the past about the only criterion utilized for the differentiation was host of origin, the morphology of organisms in the red cells of different hosts being quite similar. While our present information in regard to infectivity of given grahamellae for various host species is rather fragmentary, notable differences in cultural characteristics have been observed, so that it is perhaps best to continue to designate species for the time being at least on the basis of host of provenance. There is some indication of a considerable degree of host specificity but this matter requires further study employing culture material rather than blood for injection. Thus far the only alien host in which induced infections have become well established is closely related to the natural host. There would appear advantages in regarding grahamellae occurring naturally in such closely related hosts as varieties of a single species. It is not known to what extent the considerable number of grahamella species already described from different hosts will eventually be found to deserve specific rank. Agglutination tests, made possible by isolation in culture of grahamellae from various hosts, may possibly aid in the differentiation of species.

In regard to the relative infectivity of blood showing grahamellae and of such organisms grown in culture, the latter material appears to be more certainly infective, as judged by results in the relatively few animals inoculated, perhaps due to the greater dosage represented. Thus, of six deer mice and four voles inoculated with cultures, all became infected, but of four deer mice

and one vole injected with blood showing grahamellae, two deer mice failed to develop infection. That the latter were susceptible was proved by infection following the reinoculation of one with infective blood and of the other with cultured grahamellae.

In experimental grahamella infections, while the incidence of infected red blood corpuscles is relatively high soon after the organisms become microscopically demonstrable in stained blood films, the number of rods per cell at this time is low. Thus in a deer mouse inoculated with grahamella culture, no organisms were found at the end of 6 days, but 8 days after inoculation infected red cells were more numerous than in many natural infections. At this time a count of organisms in twenty-five infected cells showed the number to vary from one to 12 per cell, the average being 3.1. Fifteen days after inoculation the number of infected cells had increased to approximately double the number seen at 8 days, the number of organisms per infected cell varying from one to 18, with an average of 8.2 per cell. In red blood corpuscles showing a single rod, this is often found at the margin which here shows an indentation, as though the organisms had sunk into the substance of the cell. On the first appearance of grahamellae in the blood of the infected animal, isolated extracellular organisms are occasionally encountered, and, while it is possible that these have been liberated from cells crushed in the preparation of the blood film, they may represent organisms occurring free in the plasma. Groups of free grahamellae seen in stained films are obviously derived from crushed cells. Grahamellae liberated from the red cell retain their normal size and shape and never show the flattening and distortion so frequently seen in haemobartonellae and eperythrozoon.

Grahamella-infected red cells have appeared somewhat earlier in voles following inoculation (5, 5, 7, and 14 days) than in the case of *P. leucopus novaboracensis* (7, 8, 10 and 13 days). The grahamella of *P. maniculatus gracilis* appeared in 14 days after inoculation in two animals of the same species and in 9 and 14 days respectively in two local deer mice inoculated. A deer mouse injected with the blood of another carrying both grahamella and haemobartonella showed the former 7 days and the latter 9 days after inoculation. With the haemobartonellosis which becomes apparent on splenectomy of trapped animals carrying haemobartonella and grahamella infection, the latter usually disappears until

the haemobartonellosis has subsided, when it may again be found in the blood films. In several instances, however, the grahamella has persisted even in relatively large numbers throughout the course of rather heavy haemobartonella infections. In some natural infections in which grahamella has not been found previously, it appears on recovery from haemobartonellosis following splenectomy. In regard to the duration of grahamella infection we have no data based on isolations in culture which, as judged by cultures obtained from animals in which the organism could not be demonstrated microscopically, doubtless would be more reliable than the examination of stained blood films. Grahamella has been found in stained blood films from the local deer mouse up to 91 days, and in the vole up to 68 days after inoculation, both animals having been splenectomized. One natural infection in a splenectomized local deer mouse has persisted for 128 days from the time of first observation.

Concerning the effect of splenectomy on grahamellosis, Vassiliadis (1935) found that, while in rodents in general, splenectomy had little effect on this type of infection, in rats the incidence of animals showing microscopically apparent infection was increased from 16.5 per cent before the operation to 93 per cent by splenectomy. In the present series of splenectomies performed on voles, deer mice and shrews infected with grahamella, in only a single deer mouse has a definite increase in the number of organisms been observed. In this case the grahamellae appeared in large numbers preceding and during a light transient bartonellosis brought out by the splenectomy. Vassiliadis attempted to grow grahamella in culture, and, although observing encouraging changes during the first forty-eight hours of incubation, failed to obtain continued growth.

Haemobartonellae.—The effect of splenectomy in bringing about great multiplication of organisms of this type assists in their recognition. While it might be going too far to state that they do not occur within the red cells, their distribution over the surface of the erythrocytes, which is especially obvious with organisms projecting from the margin of these cells, is quite characteristic. Morphology is not always a reliable criterion for distinguishing this type of organism and under certain circumstances it would be difficult to identify a given rod as a haemobartonella or a grahamella, or a given ring as a haemobartonella or an eperythrozoon. Many of

the rod forms of *H. peromysci maniculati* are even more slender than those of the grahamellae studied. The pattern assumed in the distribution of individual organisms may assist in identifying the type, e.g. the spacing of the rods within the red cell in grahamella versus the concentration of haemobartonellae on some portion of the surface of the red cell. However, the distribution of eperythrozoon on the red cell is in some instances quite similar to that of haemobartonellae, but the former are found in greater numbers free from the red cells and in the early stages of infection show a predilection for reticulocytes, while haemobartonellae are usually confined to mature red cells. Multiplication forms are quite obvious in haemobartonellae but are not readily demonstrable in eperythrozoon. Both types of organism present marked flattening and distortion in ordinary stained blood films in contrast to grahamellae which retain their shape when set free from the red cells.

In view of the author's successful cultivation of grahamellae and his uniform failure in regard to the cultivation of *H. muris*, *H. peromysci*, the variety *maniculati* of the latter, and *H. blarinae*, as well as in recent attempts to cultivate *H. microti*, it may be necessary to reopen the question of the cultivation of rodent haemobartonellae. The possibility of confusion with an unrecognized grahamella or with other blood-inhabiting organisms will require consideration and the production of haemobartonellosis in clean animals by the injection of organisms propagated on artificial media over a considerable period will be essential for proof of cultivation. There is evidence indicating low survival properties in haemobartonellae. Ford and Eliot (1928) report attenuation in *H. muris* in blood kept in the ice-box for twenty-four hours after its withdrawal, while twenty-four hours at room temperature completely destroys the organism. In the present study, blood showing great numbers of *H. microti* on being kept in leptospira medium at room temperature for five days was found to have become non-infective.

The haemobartonellae are usually pathogenic to the host in which they occur on removal of the spleen. When splenectomized animals of other species are employed for susceptibility tests, the haemobartonellae studied have been found to be far less host specific than grahamellae.

Eperythrozoon.—The morphology of *E. coccoides* and that of *Haemobartonella muris*, type species of their respective genera, show markedly con-

trasting features. Nevertheless, a growing acquaintance with additional species of eperythrozoa and haemobartonellae brings to light organisms considered to be of the former type, which have coccoid and possibly rod forms, as, for example, *E. varians*, a new species here described, others that may be regarded as haemobartonellae which present an abundance of ring forms, e.g. *H. canis* and *H. microti*. Certain haemobartonellae such as *H. peromysci* and *H. peromysci maniculati* may present notable morphological transformation with excess of rings or coccoids when transferred to certain foreign hosts. Such morphological intergradation can hardly be ascribed to mixed infection for, with the haemobartonellae, the rings appear quite definitely developing within rods. The effects of splenectomy upon latent infections of the haemobartonellae and eperythrozoa, their distribution with relation to the red blood cells, response to arsenamine treatment, difficulty of cultivation, constitute characteristics common to both types of organism and suggest close phylogenetic relationship.

Summary

A comparative experimental and morphological study has been made of the grahamellae occurring in the short-tailed meadow mouse or vole, the local species of deer mouse, the gray-backed deer mouse, the short-tailed shrew, the pine mouse and a species of Peruvian mouse; the haemobartonellae of the local deer mouse, the gray-backed deer mouse, the short-tailed shrew, and the gray squirrel; and the eperythrozoa of the common albino mouse, the vole and the gray-backed deer mouse. Blood films of *Grahamella talpae*, *Haemobartonella muris* and *H. canis* have also been studied.

New species of *Grahamella*, *Haemobartonella* and *Eperythrozoon* have been described from certain small mammals. The species of grahamella described are differentiated chiefly on the basis of host of origin, but supported by differences observed in cultures isolated from the blood of various host species. Tests indicating a rather marked degree of host specificity in regard to grahamella infections are probably inconclusive except when cultures rather than blood are employed for the test injections. Further study should be given to the question of host specificity as a criterion of grahamella species. The species of haemobartonellae listed are based on

host of origin, infectivity and pathogenicity for splenectomized animals of other species, and morphology. The eperythrozoon species are likewise differentiated on host of origin and morphology, with some tests as to infectivity for alien hosts.

Culture strains of grahamellae have been isolated from the vole, the local deer mouse and the gray-backed deer mouse. Koch's postulates in regard to the production of infection by the inoculation of culture material and the recovery of the organism from the inoculated animal have been fulfilled with a culture strain from each of the three species. An organism isolated in culture from the blood of the short-tailed shrew appears to be a grahamella, although its identity is not established by test inoculations. A comparison of the grahamellae isolated in culture, with *Actinomyces muris* (*Streptobacillus moniliformis*) indicates close relationship and the inclusion of the genus *Grahamella* in the family ACTINOMYCETACEAE is proposed.

Numerous attempts to cultivate the haemobartonellae of the vole, two species of deer mice, the short-tailed shrew and the white rat have been uniformly unsuccessful.

Tests have been made as to the infectivity, of the haemobartonellae studied, for different species of animals. While certain haemobartonellae may be infective and pathogenic for splenectomized alien hosts, *H. peromysci* apparently persists for only a brief period in the non-splenectomized white mouse. The transference of haemobartonellae to certain alien hosts may result in profound morphological modification, and even in instances in which the inoculated host is closely related to the donor, notable transformations may occur.

Morphological studies of the haemobartonellae appearing after splenectomy in the blood of the local deer mouse, the gray-backed deer mouse and the short-tailed shrew have revealed features characteristic of higher fungi, i.e. the development of branching filaments from spore-like granules, with the production in some cases of rudimentary mycelia and multiplication by the formation of bead-like elements within the filament as well as by segmentation. These characters are not apparent in the type species, *Haemobartonella muris* Mayer, 1921, which shows no notable tendency to form filaments in the blood of the rat. *H. canis* Kikuth, 1928, on the other hand, presents a moderate degree of branching.

LIST OF GRAHAMELLAE, HAEMOBARTONELLAE AND EPERYTHROZOA STUDIED

Organism*	Host**	Comment
<i>G. peromysci</i> , n. sp.	<i>P. leucopus novaboracensis</i>	Grown in culture.
<i>G. peromysci maniculati</i> , n. var.	<i>P. maniculatus gracilis</i>	Grown in culture. Infective for <i>P. leucopus novaboracensis</i> .
<i>G. microti pennsylvanici</i> , n. var.	<i>M. pennsylvanicus pennsylvanicus</i>	Grown in culture.
<i>G. blarinae</i> , n. sp.	<i>Blarina brevicauda</i>	Culture obtained but not tested by inoculation.
<i>G. phyllotidis</i> , n. sp.	<i>Phyllotis darwini linatus</i>	
<i>G. sp.?</i>	<i>Pitymys pinetorum</i>	
<i>H. microti</i> Tyzzer and Weinman, 1939.	<i>M. pennsylvanicus pennsylvanicus</i>	Infective for splenectomized white mice.
<i>H. peromysci</i> , n. sp.	<i>P. leucopus novaboracensis</i>	Infective and pathogenic for splenectomized white mice, rats and voles.
<i>H. peromysci maniculati</i> , n. var.	<i>P. maniculatus gracilis</i>	Non-infective for splenectomized white mice.
<i>H. blarinae</i> , n. sp.	<i>Blarina brevicauda</i>	Infective for <i>P. leucopus novaboracensis</i> .
<i>H. sciuræ</i> , n. sp.	<i>Sciurus carolinensis leucotis</i>	Non-infective for splenectomized white mice.
<i>E. coccoides</i> Schilling, 1928.	<i>Mus decumanus albus</i>	Non-infective for non-splenectomized white mice.
<i>E. dispar</i> Bruynoghe and Vassiliadis, 1929.	<i>Arvicola (Microtus) arvalis</i> †	Slightly infective for splenectomized voles.
<i>E. varians</i> , n. sp.	<i>M. pennsylvanicus pennsylvanicus</i> <i>P. maniculatus gracilis</i>	Non-infective for splenectomized white mice (Tyzzer and Weinman, 1939). Infective for <i>P. leucopus novaboracensis</i> . Non-infective for splenectomized white mice.

* *G.* = *Grahamella*; *H.* = *Haemobartonella*; *E.* = *Eperythrozoon*.

** *P.* = *Peromyscus*; *M.* = *Microtus*.

† Species probably the same in both the European and the American vole.

Nevertheless, there would not as yet appear to be sufficient basis for the inclusion of the haemobartonellae with the higher fungi, and further classification is left until the matter of cultivation is thoroughly explored. Notwithstanding superficial resemblances of haemobartonellae to *Bartonella bacilliformis* as seen in stained blood films, it appears that there is no close phylogenetic relationship.

The injection of eperythrozoon into splenectomized hosts closely related to the host of origin has produced enduring infections but in less closely related hosts only transient infections.

Interference has been observed in connection with associated eperythrozoon and haemobartonella infections in the host in which the eperythrozoon is indigenous. The suppression of one type of infection by another is not based on immunity in the ordinary sense, for with the disappearance of the dominating organism the suppressed organism reappears. The suppressive effect in such cases may be as complete for a

period as that derived from the spleen. When eperythrozoon and haemobartonella infections are transferred to a foreign host, the former has no suppressive effect upon the latter.

The isolation in culture of several strains of filament-forming organisms from the blood of apparently normal voles is indicative of the prevalence of inapparent blood infections in this rodent in addition to the named species of organisms discussed. From the moniliform character of the filaments and from the presence of globoid bodies in great variety, the above strains resemble *Actinomyces muris* but rarely cause death when injected into mice. The study of the blood infections of small mammals emphasizes the frequency of infections maintained in nature, so perfectly adjusted to the host in which they occur as to be without appreciable injurious effect.

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THEORETICAL LIGHT CURVES OF CLOSE ECLIPSING SYSTEMS

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ABSTRACT

The aim of the present study will be to investigate the theoretical light curves of close eclipsing systems, between eclipses as well as within minima, taking account of the departures of both components from spherical shape due to their axial rotation and mutual tidal action. The distortion influences the light curves both directly, by varying the area visible at various phases, and indirectly, by rearranging the distribution of brightness over the distorted surface which, in addition to limb-darkening, should vary proportionally to the local gravity. The form of each component is supposed to be one of equilibrium under instantaneous rotational and tidal forces, and predictable theoretically so long as the axial rotation is slow and the tidal action of each star can be regarded as being due to a mass-point.

In the present paper photometric consequences of distortion of both components of an eclipsing binary will be investigated to the same degree of accuracy to which their own forms are known (*i.e.*, as far as effects of the second, third, and fourth spherical harmonic deformations are concerned). Account will be taken of the combined effects of geometrical boundary distortion as well as of limb-darkening and gravity-darkening at any particular frequency of light. The components will be supposed to describe circular orbits; no notice will be taken of complications that would arise from orbital eccentricity. After a brief general survey (sec. I), equations of the problem are set up (sec. II) and reduced to tractable forms (sec. III). Photometric implications of the gravity-darkening will prove relatively most troublesome and a special class of functions will be introduced (sec. IV) to deal efficiently with this particular part of the problem. The explicit forms of the theoretical light curves are then given in section V in terms of certain integrals which are subsequently evaluated in a finite number of terms (sec. VI). The concluding section VII will be devoted to a more general discussion concerning the "rectification" of light curves and the application of the preceding results to practical cases. It is pointed out that assumptions conventionally associated with the process of rectification are not generally fulfilled, and more appropriate procedures are developed.

The results of the present paper should, apart from the reflection effect, give a complete representation of the theoretically expected changes of light of close eclipsing systems between minima as well as within eclipses—regardless of whether the star undergoing eclipse is the larger or the smaller of the two and whether the eclipse is partial or annular.

I. INTRODUCTION

1. A general task of determining the elements of eclipsing binary systems from an analysis of their light curves necessarily requires a knowl-

edge of the loss of light, during eclipse, for any relative position of the components. This evidently depends on the form of both components as well as on the distribution of brightness over the disk of the eclipsed star. For spherical components with uniform or radially-symmetrical distribution of brightness the relation between the geometry of eclipse and the corresponding loss of light is well known. The reality, however, is likely to be more complex. Unless the stars were rigid, the components of binary systems can be regarded as approximately spherical only if their dimensions, expressed in terms of their separation, are very small. If, however, the components are brought closer together, their surfaces will deviate from a sphere, on account of

- (a) the rotational distortion,
- (b) the mutual tidal action.

Provided that stars behave as fluid bodies whose periods of free oscillation are short compared with the period of the binary orbit,¹ the tidal distortion of both components will be given by the equilibrium theory of tides and is at present accurately predictable as far as the disturbing action of one component upon the other can be regarded as that of a mass-point. The rotational distortion can be predicted to the same degree of accuracy provided that the axes of rotation are constantly perpendicular to the orbital plane. In the case of components revolving in circular orbits we may legitimately assume that their surface layers rotate with the Keplerian angular velocity; whether or not their interiors rotate in this way is largely irrelevant as far as the external form of the components is concerned.²

The problem which we propose to attack and solve in the present investigation can be briefly stated as follows: *Let us consider a close binary system, the components of which describe circular orbits in a plane inclined to the line of sight so that the components eclipse each other alternately at the time of conjunction. Both stars are distorted by*

¹ Cf. *e.g.*, Sterne, *M.N.*, **99**, 662, 1939.

² Cf. Kopal, *Proc. Nat. Acad. Sci.*, **27**, 359, 1941.

axial rotation with Keplerian angular velocity and by mutual tidal action. The outward flux of radiant energy at the surface of the distorted components varies proportionally to the local gravity.³ It is to investigate the changes of light exhibited by such systems in any particular frequency of light, and to the same degree of accuracy to which the form of both components is known. The changes of light displayed by such systems between minima have recently become a subject of numerous papers;⁴ but changes of light within eclipses—a geometrically much more complicated phenomenon—are as yet but very incompletely known and remain to be investigated. In the present paper such an investigation will be made.

The effects, upon light curves, of the distortion of both components can be regarded as consisting of two parts:

- (1) effects arising from the distortion of the eclipsing component,
- (2) effects due to the distortion of the eclipsed star.

Effects of the former kind act through the distortion of the shadow cylinder cast by the eclipsing body, and have previously been studied under certain restricted conditions by Walter⁵ and Russell,⁶ and more generally by Takeda⁷ and Kopal.⁸ They are geometrical in nature and relatively simple. On the other hand, effects mentioned in (2) involve also physical considerations (law of radiation) and are vastly more complex. This is because in dealing with photometric effects of distortion of the star undergoing eclipse—which will consistently be referred to as the *primary component*—we have not only to take account of the distorted geometry, but also its effects upon the distribution of brightness over the eclipsed portion of the primary's disk. For it is well known that the distribution of brightness can be regarded as uniform or radially-symmetrical (limb-darkening) only if a star is spherical or very nearly so; but if it gets appreciably distorted, the distribution of brightness over its surface should, in addition to limb-darkening, vary proportionally to the local gravity.³ Re-

cent investigations of the ellipticity effect in close eclipsing systems⁹ have established the reality of the gravity-effect upon the distribution of surface brightness in distorted stars beyond any doubt, and in the amount theoretically expected. It therefore appears that no substantial advance in our knowledge of close binary systems can be made unless the bearing of the gravity-effect upon the light curves within minima is investigated in detail. This sets the task which we are going to face.

Its inherent complexity has probably been discouraging for most investigators so far, and the only existing attempt at its solution appears to be that by Takeda.⁷ The starting points of Takeda's and of the present paper will necessarily have many features in common; in particular, the transformation of coördinates which we shall employ in section III of the present paper has also been used by Takeda. The present investigation will, however, be considerably more general in scope. Takeda's aim has been to study variation of integrated light of eclipsing systems with components built up according to the standard model (in point of fact, Takeda's coefficients pertaining to the tidal distortion correspond to a mass-point model). A centrally condensed model offers probably an ample approximation for most of the real eclipsing systems. As will be shown later in more detail, however, the restriction to bolometric light changes is decidedly inadequate and would render Takeda's results of little value for application to actual light curves observed in more or less narrow spectral ranges. In addition, Takeda did not evaluate the forms of the theoretical light curves explicitly, but expressed them in terms of certain integrals the solution of which was largely left as an exercise to the reader. In the present paper our aim will be to evaluate in a finite number of terms the changes of light due to the eclipses of distorted stars of any internal structure, and observed in any particular frequency of light; and the analysis will include effects of the second, third, and fourth spherical harmonic deformations of both components due to their own rotation and mutual tidal action.

II. EQUATIONS OF THE PROBLEM

2. The loss of light, during eclipse, as seen by an observer at a great distance, can generally be

³ Cf. von Zeipel, *M.N.*, **84**, 665, 684, 702, 1924; and Chandrasekhar, *M.N.*, **93**, 571–573, 1933.

⁴ Takeda, *Kyoto Mem.*, **A**, **18**, 197, 1934; Russell, *Ap.J.*, **90**, 641, 1939; Kopal, *Ann. New York Acad. Sci.*, **41**, 13, 1941; Sterne, *Proc. Nat. Acad. Sci.*, **27**, 99, 1941.

⁵ *Königsberg Veröff.*, No. 2, p. 28, 1931.

⁶ *Ap.J.*, **90**, 641, 1939.

⁷ *Kyoto Mem.*, **A**, **20**, 47, 1937.

⁸ *Ap.J.*, **94**, 159, 1941.

⁹ Russell, *Ap.J.*, **90**, 641, 1939; or Kopal, *Ann. New York Acad. Sci.*, **41**, 13, 1941.

expressed as

$$\Delta\mathcal{Q} = \int_S J \cos \gamma \, d\sigma, \quad (1)$$

where J denotes the intensity at any point of the surface of the eclipsed star; γ , the angle of foreshortening; and the surface element $d\sigma$ is evidently given by

$$\cos \beta \, d\sigma = r^2 \sin \theta \, d\theta \, d\phi;$$

θ, ϕ being polar coördinates taken with respect to a rectangular system the X -axis of which is constantly coincident with the line joining the centers of both components, and Z with that of rotation of the primary star (the center of which is taken as origin). The angle β is one between a radius-vector and a normal to the surface $r(\theta, \phi)$ specifying the boundary of the distorted primary star. The range of integration S is to be extended over the whole eclipsed area (for which $\cos \gamma$ is positive).

The angles β and γ are clearly defined by

$$\cos \beta = \lambda l + \mu m + \nu n, \quad (2)$$

$$\cos \gamma = l_0 + m m_0 + n n_0, \quad (3)$$

where

$$\begin{array}{ccc} \lambda, & \mu, & \nu \\ l, & m, & n \\ l_0, & m_0, & n_0 \end{array}$$

denote direction cosines of a radius-vector, surface normal, and line of sight, respectively.

The values of λ, μ, ν and l_0, m_0, n_0 depend upon the adopted frame of reference and the observer's position. In conformity with the preceding we have

$$\begin{aligned} \lambda &= \cos \phi \sin \theta, \\ \mu &= \sin \phi \sin \theta, \\ \nu &= \cos \theta, \end{aligned} \quad (4)$$

where ϕ denotes the angle, in the XY plane, between the projected radius-vector and the X -axis; and θ is the angle between a radius-vector and the Z -axis. Similarly,

$$\begin{aligned} l_0 &= \cos \psi \sin i, \\ m_0 &= \sin \psi \sin i, \\ n_0 &= \cos i, \end{aligned} \quad (5)$$

where ψ denotes the mean anomaly in the plane of the orbit (phase angle), and i , the inclination of the orbital plane to the celestial sphere.

3. The values of the remaining direction cosines l, m, n depend on the form of the free surface of the distorted primary star. If the latter is in equilibrium under the forces exerted upon it by its own rotation and by the tidal pull of the

eclipsing companion, its form can at present be predicted as far as the disturbing action of the companion can be regarded as that of a mass-point. Further, if the primary component rotates about a fixed axis perpendicular to the orbital plane with Keplerian angular velocity, the rotational distortion—to this order of accuracy—takes the form

$$-\frac{1}{3} \left(1 + \frac{m_2}{m_1} \right) \Delta_2 r_1^3 P_2(\nu), \quad (6)$$

and the tidal distortion becomes

$$+ \frac{m_2}{m_1} \sum_{j=2}^4 \Delta_j r_1^{j+1} P_j(\lambda), \quad (7)$$

where m_2/m_1 denotes the mass-ratio; r_1 , the radius of a sphere having the same volume as the distorted primary star and expressed in terms of the radius of circular orbit; and the P_j 's are Legendre polynomials of various orders. The Δ_j 's are numerical constants depending on the internal structure (density distribution) of the distorted star and are generally defined by

$$\Delta_j = \frac{2j+1}{j + \eta_j(r_1)}, \quad (8)$$

where $\eta(r_1)$ is the surface value of a function defined by the differential equation

$$r \frac{d\eta_j}{dr} + \eta_j(\eta_j - 1) + 6 \frac{\rho}{\bar{\rho}} (\eta_j + 1) = j(j+1),$$

which is due to Radau.¹⁰ Here ρ denotes the density at any point in the interior of the distorted star while $\bar{\rho}$ is the mean density interior to r .

The numerical values of the Δ_j 's depend in principle on the whole march of density distribution. In practice, however, they turn out to be almost uniquely specified by the ratio of the central to the mean density (density condensation) of a given configuration.¹¹ Except for a few special cases Radau's equation does not admit of a solution in a closed form and has to be integrated numerically. The most complete integrations are so far available for the polytropic family of models,¹² and the results are compiled in the following Table 1.

¹⁰ *Comptes Rendus*, 100, 972, 1885; cf. also Tisserand, *Traité de Mécanique Céleste*, Tome II, p. 221, Paris 1891. Radau derived his equation for the special case of $j = 2$.

¹¹ Cf. Kopal, *M.N.*, 98, 414, 589, 1938; or Sterne, *M.N.*, 99, 662, 1939 (p. 664, footnote).

¹² Chandrasekhar, *M.N.*, 93, 449, 1933 (Table VI). Chandrasekhar's results were obtained by numerical integration of less general equations.

TABLE 1

Poly- tropic Index n	0	1	1.5	2	3	4	5
ρ_c/ρ_m	1	3.28987	5.9907	11.4025	54.1825	622.408	∞
$\eta_2(r_1)$	0	1.28986	1.8784	2.3546	2.8596	2.98669	3
Δ_2	2.5	1.51982	1.2892	1.1482	1.0289	1.00267	1
$\eta_3(r_1)$	1	2.77124	3.3183	3.6743	3.94887	3.99672	4
Δ_3	1.75	1.21291	1.1079	1.0488	1.00736	1.00047	1
$\eta_4(r_1)$	2	4.03228	4.5211	4.7968	4.97480	4.99874	5
Δ_4	1.5	1.12048	1.0562	1.0231	1.00281	1.00014	1

The direction cosines of a line normal to the distorted surface specified by (6) and (7) then are

$$l = \lambda \left\{ 1 - v_1^{(2)} v^2 + \left(\lambda - \frac{1}{\lambda} \right) \sum_{j=2}^4 w_1^{(j)} P_j'(\lambda) \right\},$$

$$m = \mu \left\{ 1 - v_1^{(2)} v^2 + \lambda \sum_{j=2}^4 w_1^{(j)} P_j'(\lambda) \right\}, \quad (9)$$

$$n = \nu \left\{ 1 - v_1^{(2)} v^2 + v_1^{(2)} + \lambda \sum_{j=2}^4 w_1^{(j)} P_j'(\lambda) \right\},$$

where accents on P_{j-1} denote derivatives with respect to λ , and where we have abbreviated ¹²

$$v_{1,2}^{(2)} = \left(1 + \frac{m_{2,1}}{m_{1,2}} \right) \Delta_2 r_{1,2}^2,$$

$$w_{1,2}^{(j)} = \frac{m_{2,1}}{m_{1,2}} \Delta_j r_{1,2}^{j+2}. \quad (10.0)$$

Both v and w are evidently small quantities of the first order which specify the amount of distortion. As the reader may easily verify the angle β between a radius-vector and surface normal is of the same order of magnitude as the distortion itself; i.e., a small quantity of the first order. Hence, within the scheme of our approximation, the squares and higher powers of β can be neglected and $\cos \beta$ reduces to unity. The angle of foreshortening γ is then obtained from (3) as

$$\cos \gamma = L \left\{ 1 + \frac{1}{3} v_1^{(2)} \left[\frac{n_0}{L} - v \right] P_2'(\nu) - \left[\frac{I_0}{L} - \lambda \right] \sum_{j=2}^4 w_1^{(j)} P_j'(\lambda) \right\}, \quad (3.1)$$

¹² If the eclipsed primary star does not rotate with the Keplerian angular velocity (which is unlikely for systems revolving in circular orbits), but with an independent angular velocity ω , then

$$v_1^{(2)} = \frac{3}{2} \Delta_2 \frac{\omega^2}{2\pi G \rho_m},$$

where G is the gravitation constant and ρ_m the mean density of the rotating star.

where

$$L = \lambda_0 + \mu m_0 + \nu n_0.$$

4. The expression for J remains to be specified. The effects of darkening at limb should, with sufficient accuracy, be satisfied by the well-known cosine law

$$J = H(1 - u + u \cos \gamma),$$

where H denotes the intensity of radiation parallel to the line of sight and u the coefficient of limb darkening.

As regards H , a theorem was proved by von Zeipel¹⁴ that the outward flux of total radiation (i.e., bolometric surface brightness) over the surface of a distorted star in hydrostatic equilibrium must be proportional to the local gravity. The proof of the theorem presumes that stars rotate with uniform angular velocity and that there are no appreciable convection currents beneath the photosphere. It does not seem likely that deviations from uniform rotation could materially change the theorem; but an appreciable transport of heat by material currents may make the flow of heat no longer proportional to the temperature gradient and so render the theorem invalid. It is difficult to predict solely on the theoretical basis to which extent von Zeipel's theorem should apply to actual stars; but its consequences upon changes of light exhibited by close eclipsing systems between minima (ellipticity effect) were recently found exactly in agreement with the observed facts.⁹ Hence the application of the theorem to reality seems fully justified and we have to put

$$\frac{H - H_0}{H_0} = \frac{g - g_0}{g_0}, \quad (12)$$

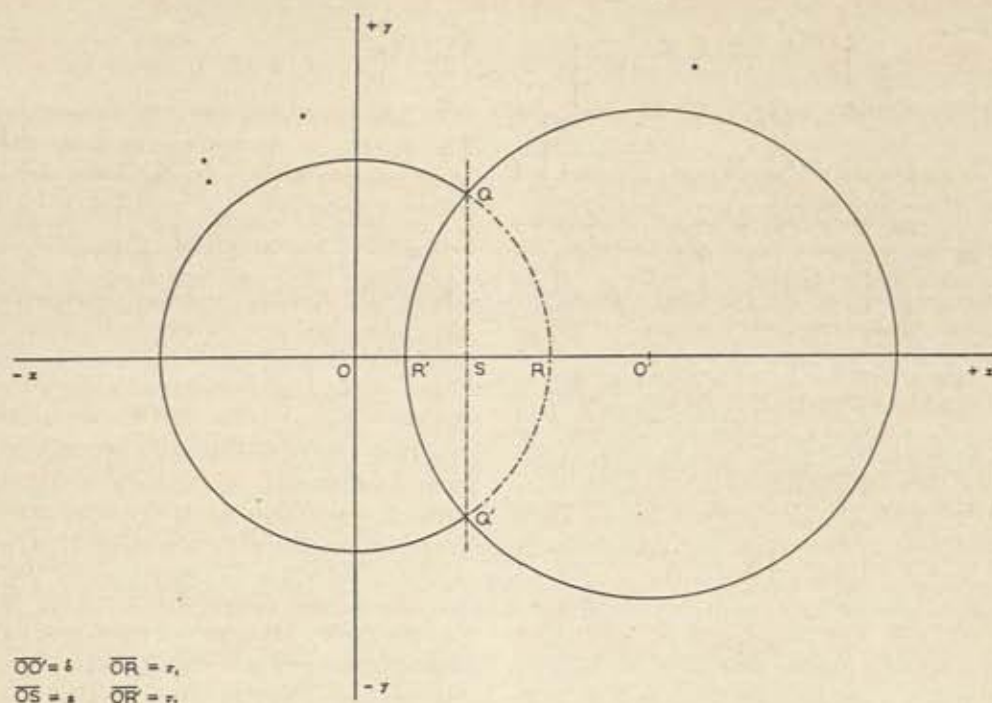
where g and g_0 denote the local and mean surface gravity, respectively, and H_0 is the bolometric surface brightness at a point where $g = g_0$.

If the star undergoing eclipse radiates like a black body, equation (12) can evidently be rewritten as

$$\frac{g - g_0}{g_0} = \frac{T^4 - T_0^4}{T_0^4}, \quad (13)$$

where T denotes the local effective temperature and T_0 the mean effective temperature averaged over the whole disk. Equation (13) governs the variation of temperature over the surface of a

¹⁴ *M.N.*, **84**, 665, 684, 702, 1924. Cf. also Chandrasekhar, *M.N.*, **93**, 539, 1933 (Appendix I); or Sterne, *Proc. Nat. Acad. Sci.*, **27**, 99, 1941.



distorted star. The surface brightness at any single wave length λ varies as

$$\frac{H}{H_0} = \frac{e^{c_2/\lambda T_0} - 1}{e^{c_2/\lambda T} - 1}, \quad (14.0)$$

where $c_2 = 1.432$ cm.deg. If we substitute in (14.0) for T from (13) and expand the former in a Taylor series in the neighborhood of $T = T_0$ then, to the first order in small quantities, equation (14.0) reduces to

$$\frac{H}{H_0} = 1 - \tau \left(1 - \frac{g}{g_0} \right), \quad (14.1)$$

where

$$\tau = \frac{c_2}{4\lambda T_0(1 - e^{-c_2/\lambda T_0})}. \quad (15)$$

If $\tau = 1$ (i.e., $\lambda T_0 = 0.3652$ cm.deg.) equation (14.1) gives the intensity distribution for total radiation. In practical cases, however, τ may be either greater or smaller than unity. A glance at (15) shows that if $(c_2/\lambda T_0)$ is small (high temperatures or long wave lengths) τ converges to one fourth; while if $(c_2/\lambda T_0)$ is large, τ varies proportionally to it. A three-decimal table of 4τ in terms of λ and T_0 has recently been prepared by the writer.¹⁵

The surface gravity of a star the distortion of which is specified by (6) and (7) can be shown¹⁶ to vary as

$$\frac{g - g_0}{g_0} = \frac{1}{3}v_1^{(2)} \left\{ \frac{5}{\Delta_2} - 1 \right\} P_2(v) - \sum_{j=2}^{\infty} \left\{ \frac{2j+1}{\Delta_j} - j+1 \right\} w_1^{(j)} P_j(\lambda). \quad (16)$$

Inserting this in (14.1) we obtain the proper distribution of brightness due to the gravity effect.

5. The fractional loss of light ΔQ within minima can evidently be expressed as

$$\Delta Q = \frac{3(1-u)}{3-u} \Delta Q^U + \frac{2u}{3-u} \Delta Q^D, \quad (17.0)$$

where ΔQ^U and ΔQ^D denote the "uniform" and "completely darkened" fractional losses of light defined by

$$\pi r_1^2 H_0 \Delta Q^U = \int_S r^2 H \cos \gamma \sin \theta d\theta d\phi, \quad (18.0)$$

and

$$\pi r_1^2 H_0 \Delta Q^D = \frac{3}{2} \int_S r^2 H \cos^2 \gamma \sin \theta d\theta d\phi. \quad (18.1)$$

If we now combine equations (3.1), (6), (7), (14.1) and (16) the integrand of (18.0) takes the

¹⁶ Cf. Chandrasekhar, *M.N.*, **93**, 539, 1933 (Equation 123).

¹⁵ *Ann. New York Acad. Sci.*, **41**, 13, 1941 (Table 2).

neat form

$$r^2 H \cos \gamma = r_1^2 H_0 L \left\{ 1 + \frac{1}{3} v_1^{(2)} \left[\left\{ \tau \left(\frac{5}{\Delta_2} - 1 \right) - 2 \right\} P_2(\nu) + \left\{ \frac{n_0}{L} - \nu \right\} P_2'(\nu) \right] - \sum_{j=2}^4 w_1^{(j)} \left[\left\{ \tau \left(\frac{2j+1}{\Delta_j} + 1 - j \right) - 2 \right\} P_j(\lambda) + \left\{ \frac{l_0}{L} - \lambda \right\} P_j'(\lambda) \right] \right\}, \quad (19.0)$$

while for darkened disks

$$r^2 H \cos^2 \gamma = r_1^2 H_0 L^2 \left\{ 1 + \frac{1}{3} v_1^{(2)} \left[\left\{ \tau \left(\frac{5}{\Delta_2} - 1 \right) - 2 \right\} P_2(\nu) + 2 \left\{ \frac{n_0}{L} - \nu \right\} P_2'(\nu) \right] - \sum_{j=2}^4 w_1^{(j)} \left[\left\{ \tau \left(\frac{2j+1}{\Delta_j} + 1 - j \right) - 2 \right\} P_j(\lambda) + 2 \left\{ \frac{l_0}{L} - \lambda \right\} P_j'(\lambda) \right] \right\}. \quad (19.1)$$

If we consider effects of total radiation only, and assume the distorted star to be a centrally condensed one, the $\tau = 1$ and an inspection of Table 1 reveals that the Δ_j 's may be put equal to unity without any appreciable error. Making use of the identity

$$\lambda P_j'(\lambda) = j P_j(\lambda) + P_{j-1}'(\lambda)$$

the right-hand side of (19.0) reduces to

$$r_1^2 H_0 L \left\{ 1 + \frac{1}{3} v_1^{(2)} \left[\frac{n_0}{L} P_2'(\nu) - 1 \right] - \sum_{j=2}^4 w_1^{(j)} \left[\frac{l_0}{L} P_j'(\lambda) - P_{j-1}'(\lambda) \right] \right\}, \quad (19.01)$$

and that of (19.1) can be simplified in an analogous way. To this degree of approximation the problem has been dealt with by Takeda.⁴ We note, however, that while an assumption $\Delta_j \approx 1$ offers a satisfactory approximation in the majority of practical cases, τ may happen to be considerably in excess of, or smaller than, unity; so that $|\tau - 1|$ cannot in general be regarded a small quantity. Hence the scheme of approximation adopted by Takeda appears inadequate, and more complete expressions (19.0) and (19.1) with an appropriate value of τ are to be employed.

III. TRANSFORMATION OF COÖRDINATES

6. In the preceding section the integrands of (18.0) and (18.1) have been expressed in terms of polar coördinates referred to a fixed rectangular frame XYZ , with origin at the center of the eclipsed star, and axes parallel with the three principal axes of the distorted ellipsoid. In order to be able to carry out the integration we still have to specify the limits. In doing so, we soon discover that a fixed "astrocentric" system of coördinates is unsuitable for the study of light changes within minima; the limits result too

complicated and the respective integrals become almost intractable. As will be shown below, however, this difficulty can be avoided by a suitable change of coördinates.

Let us change over to a moving rectangular system $X'Y'Z'$ having the same origin, but with the X' -axis now constantly coincident with the line of sight and the Z' -axis in the direction of the projected center of the secondary component. The new primed axes, referred to the original system, are then clearly specified by the scheme

	X'	Y'	Z'
X	l_0	l_1	l_2
Y	m_0	m_1	m_2
Z	n_0	n_1	n_2

where the direction cosines of the respective axes are:

$$l_0 = \cos \psi \sin i, \quad l_1 = 0, \quad l_2 = \sqrt{1 - l_0^2},$$

$$m_0 = \sin \psi \sin i, \quad m_1 = -\frac{n_0}{\sqrt{1 - l_0^2}},$$

$$m_2 = -\frac{l_0 m_0}{\sqrt{1 - l_0^2}}, \quad (20)$$

$$n_0 = \cos i, \quad n_1 = \frac{m_0}{\sqrt{1 - l_0^2}},$$

$$n_2 = -\frac{l_0 n_0}{\sqrt{1 - l_0^2}}.$$

The coördinates of the projected center of the eclipsing component before maximum eclipse are assumed to be positive.

The eclipsed portion of the primary's disk can now be specified as follows. The equation of the shadow cylinder cast by the secondary component in the direction of the line of sight in the primed system becomes

$$(\delta - Z')^2 + Y'^2 = r_2^2(1 + \Delta\bar{r}_2)^2, \quad (21)$$

where r_2 is the fractional radius of a sphere having the same volume as the eclipsing star; $\Delta\bar{r}_2$ is a measure of deformation of the secondary's shadow cylinder in the $Y'Z'$ -plane; and δ , the projected distance of centers of the two components in the same plane is clearly given by

$$\delta^2 = \sin^2 \psi \sin^2 i + \cos^2 i.$$

The radius of the orbit is taken as our unity of length.

The equation of surface of the distorted primary star admits evidently of the parametric representation

$$\begin{aligned} X' &= r_1(1 + \Delta r_1)L, \\ Y' &= r_1(1 + \Delta r_1)M, \\ Z' &= r_1(1 + \Delta r_1)N, \end{aligned} \quad (22)$$

where Δr_1 is a measure of distortion of the primary component, and L, M, N are direction cosines of any radius-vector in the primed system, related with the direction cosines λ, μ, ν of the fixed system by means of

$$\begin{aligned} \lambda &= l_0L + l_1M + l_2N, \\ \nu &= n_0L + n_1M + n_2N. \end{aligned} \quad (23)$$

The direction cosines L, M, N can evidently be regarded as rectangular coordinates in the primed system over a sphere of unit radius. We prefer, however, consistently with the preceding, to adopt the radius of the orbit as our unity of length. Let us therefore put

$$L = \frac{z}{r_1}, \quad M = \frac{y}{r_1}, \quad N = \frac{x}{r_1}, \quad (24)$$

and adopt x, y, z as our new independent variables. By virtue of (23) the Legendre coefficients $P_2(\nu)$ or $P_j(\lambda)$, associated with effects of the rotational and tidal distortion, can now be rewritten as polynomials of the j -th degree in terms of integral powers of x, y, z , with coefficients depending upon the amount of distortion and the relative position of the components in their orbit. Since, further,

$$\sin \theta d\theta d\phi = \frac{dx dy}{r_1 \sqrt{r_1^2 - x^2 - y^2}},$$

the whole integrand of (18.0) or (18.1) in terms of the new variables clearly becomes an algebraic function of x, y , and z —the general terms arising from the rotational and tidal distortion being of the form

$$x^m y z^n \quad \text{and} \quad x^m z^n,$$

respectively, where $m \geq 0$ and $n \geq -1$.

7. The range of integration can now be found as follows. The direction cosines L, M, N are known to satisfy the relation

$$L^2 + M^2 + N^2 = 1.$$

It may be remembered that L , the cosine of the angle of foreshortening, vanishes at the limb of the primary's disk if the latter is undistorted, and becomes a small quantity in the case of distortion, the square of which can be neglected. Hence, to the order of accuracy we are working, the intersection of the surface of the primary component with the xy -plane reduces to

$$x^2 + y^2 = r_1^2, \quad (25)$$

and thus the arc QRQ' limiting the eclipsed fraction in the xy -plane (see Fig. 1) can be considered a circle.

The equation of the remaining arc $QR'Q'$ can be obtained by solving the equation of the shadow cylinder with that of the surface of the eclipsed star. If we insert (22) in (21) then, to the first order in small quantities, the equation of $QR'Q'$ becomes

$$(\delta - x)^2 + y^2 = r_2^2(1 + 2\Delta\bar{r}_2 - 2\Delta r_1\{r_2^2 - \delta(\delta - x)\} + \dots) \quad (26)$$

Now, to the same order of approximation, expressions (6) and (7) yield

$$\Delta r_1 = \sum_{j=2}^4 w_1^{(j)} P_j(\lambda) - \frac{1}{3} v_1^{(2)} P_2(\nu), \quad (27)$$

where

$$\begin{aligned} r_1 \lambda &= l_0 \sqrt{2\delta(s - x)} + l_2 x, \\ r_1 \nu &= n_0 \sqrt{2\delta(s - x)} \\ &\quad + n_1 \sqrt{r_2^2 - (\delta - x)^2} + n_2 x, \end{aligned} \quad (28)$$

and

$$s = \frac{r_1^2 - r_2^2 + \delta^2}{2\delta}. \quad (29)$$

Further, the corresponding distortion of the shadow cylinder cast by the secondary component takes the form

$$\Delta\bar{r}_2 = \sum_{j=2}^4 w_2^{(j)} P_j(\lambda') - \frac{1}{3} v_2^{(j)} P_2(\nu'), \quad (30)$$

where, since the line of sight is tangent to the boundary of the shadow cylinder,

$$\begin{aligned} r_2 \lambda' &= l_2(\delta - x), \\ r_2 \nu' &= n_1 \sqrt{r_2^2 - (\delta - x)^2} + n_2(\delta - x). \end{aligned} \quad (31)$$

The deviation, in the y -coördinate, of arc $QR'Q'$ from the circle

$$(\delta - x)^2 + y^2 = r_2^2 \quad (32)$$

then results

$$\begin{aligned} \Delta y &= \frac{r_2^2 \Delta \bar{r}_2}{\sqrt{r_2^2 - (\delta - x)^2}} - \{r_2^2 \\ &\quad - \delta(\delta - x)\} \frac{\Delta r_1}{\sqrt{r_2^2 - (\delta - x)^2}} + \dots \end{aligned} \quad (33)$$

8. The limits of integration specifying the eclipsed portion of the primary's disk then result as follows. Let us divide the total eclipsed area in two parts: $QRQ'S$ and $QR'Q'S$ (Fig. 1). The light lost by the eclipse of $QRQ'S$ does not depend explicitly upon the radius of the eclipsing star and can be obtained by integrating (18.0) or (18.1) between $\pm \sqrt{r_1^2 - x^2}$ in the y -coördinate, and from s to r_1 in the x -coördinate. The loss of light due to the eclipse of $QR'Q'S$ can—apart from effects of geometrical boundary distortion—be found by integrating the same integrand between $\pm \sqrt{r_2^2 - (\delta - x)^2}$ in the y -coördinate, and from $(\delta - r_2)$ to s in the x -coördinate. If the primary star is the larger of the two and

$s > r_1$, the eclipse becomes annular. The segment $QRQ'S$ then evidently vanishes, and the loss of light is obtained by integrating between $\pm \sqrt{r_2^2 - (\delta - x)^2}$ in the y -coördinate, and between $(\delta \pm r_2)$ in the x -coördinate.

Effects of distortion of the arc $QR'Q'S$ can, to the order of accuracy we are working, be finally obtained by a single integration of Δy with respect to x , taken also from $(\delta - r_2)$ to s if the eclipse is partial, and from $(\delta - r_2)$ to $(\delta + r_2)$ if it is annular. If the disk of the star undergoing eclipse is uniformly bright, the integrand consists solely of $2\Delta y$; if it is completely darkened at limb, $3\Delta y$ is to be multiplied by the foreshortening factor $\sqrt{2\delta(s - x)}$. Since Δy is a small quantity of the first order itself, the effects of gravity-darkening are clearly negligible in this connection.

Let us, following Takeda, denote terms obtained by double integration with respect to x and y within circular limits as "circular integrals," and those resulting from a single integration of Δy with respect to x as "boundary corrections." As is evident from equation (33), the latter will consist of two parts, one involving $\Delta \bar{r}_2$ which depends on the distortion of the eclipsing component, and the other involving Δr_1 which depends on the distortion of the eclipsed star. Our task will be to investigate both in turn.

IV. ASSOCIATED ALPHA-FUNCTIONS

9. In the preceding section we were led to express the changes of light due to the eclipse of a distorted star in terms of circular integrals defined as

$$\pi r_1^{m+n+2} \alpha_n^m = \left\{ \int_s^{r_1} \int_{-\sqrt{r_1^2 - x^2}}^{+\sqrt{r_1^2 - x^2}} + \int_{\delta - r_2}^s \int_{-\sqrt{r_2^2 - (\delta - x)^2}}^{+\sqrt{r_2^2 - (\delta - x)^2}} \right\} x^m z^n dx dy \quad (34.0)$$

if the eclipse is partial, and

$$\pi r_1^{m+n+2} \alpha_n^m = \int_{\delta - r_2}^{\delta + r_2} \int_{-\sqrt{r_2^2 - (\delta - x)^2}}^{+\sqrt{r_2^2 - (\delta - x)^2}} x^m z^n dx dy \quad (34.1)$$

if it is annular; where

$$z = \sqrt{r_1^2 - x^2 - y^2}.$$

We propose to call the dimensionless quantities defined by the preceding equations *associated α -functions* of the order m and index n . As the reader may easily verify, the two lowest such functions of zero order possess familiar meaning: α_0^0 represents the fractional loss of light due to the eclipse of an uniformly bright circular disk (equal to the fractional area eclipsed), while $\frac{2}{3}\alpha_1^0$ gives the same loss of light if the eclipsed disk is completely darkened at limb. In the case of incomplete limb-darkening the corresponding loss of light can always be obtained as a certain weighted mean of

α_0^0 and α_1^0 ; but associated α -functions of higher orders and indices are required to account for effects of gravity-darkening. Thus in the present section our task will be to investigate the properties of such functions and integrate equations (34) for any value of m and n in a finite number of terms.

It is convenient, for this purpose, to split equation (34.0) in two parts by putting

$$\pi r_1^{m+n+2} \alpha_n^m = \mathfrak{A}_n^m + \mathfrak{B}_n^m, \quad (34.01)$$

where

$$\mathfrak{A}_n^m = \int_s^{r_1} \int_{-\sqrt{r_1^2-x^2}}^{+\sqrt{r_1^2-x^2}} x^m y^n dx dy, \quad (35)$$

$$\mathfrak{B}_n^m = \int_{\delta-r_2}^s \int_{-\sqrt{r_2^2-(\delta-x)^2}}^{+\sqrt{r_2^2-(\delta-x)^2}} x^m y^n dx dy, \quad (36)$$

and to deal with each in turn. For annular eclipses, equation (34.1) can likewise be written as

$$\pi r_1^{m+n+2} \alpha_n^m = \mathfrak{B}_n^m, \quad (34.11)$$

provided that s is replaced by $(\delta + r_2)$ in the limits of integration on the right-hand side of (36).

As to \mathfrak{A} , integrating we obtain at once that

$$\begin{aligned} \mathfrak{A}_n^m &= B\left(\frac{1}{2}, 1 + \frac{1}{2}n\right) \int_s^{r_1} x^m (r_1^2 - x^2)^{(n+1)/2} dx \\ &= B\left(\frac{1}{2}, 1 + \frac{1}{2}n\right) \{D_{n+1}^m(r_1) - D_{n+1}^m(s)\}, \end{aligned} \quad (37)$$

where $B(m, n)$ denotes the complete beta-functions (numerical factors), and

$$D_{2\nu}^m(x) = \int_0^x x^m (r_1^2 - x^2)^\nu dx,$$

which is a binomial integral tractable by elementary means.

The calculation of \mathfrak{B}_n^m proves more tedious. Integrating with respect to y we find that for n zero or an even integer

$$\mathfrak{B}_{2\nu}^m = \frac{1}{\pi} B\left(\frac{1}{2}, 1 + \nu\right) \sum_{j=0}^{\nu} B\left(\frac{1}{2}, \frac{1}{2} + \nu - j\right) I_{2j, 1, 2(\nu-j)}^m; \quad \nu = 0, 1, 2, \dots \quad (38.0)$$

while if n is odd,

$$\mathfrak{B}_{2\nu-1}^m = \frac{1}{\pi} B\left(\frac{1}{2}, \frac{1}{2} + \nu\right) \left\{ \sum_{j=1}^{\nu} B\left(\frac{1}{2}, j\right) I_{2j-1, 1, 2j-1}^m + 2\Pi_{2\nu}^m \right\}, \quad (38.1)$$

where

$$I_{2\alpha, \beta, \gamma}^m = \int_{\delta-r_2}^{\delta} (r_1^2 - x^2)^\alpha [r_2^2 - (\delta - x)^2]^\beta [2\delta(s - x)]^{\gamma/2} x^m dx, \quad (39)$$

and

$$\Pi_{2\nu}^m = \int_{\delta-r_2}^{\delta} x^m (r_1^2 - x^2)^\nu \sin^{-1} \sqrt{\frac{r_2^2 - (\delta - x)^2}{r_1^2 - x^2}} dx, \quad (40)$$

where $\delta = s$ or $(\delta + r_2)$ as to whether the eclipse is partial or annular. These are the two standard forms which we have to solve.

10. The methods of integration of (39) depend in principle upon the values of the three subscripts α, β, γ . The first can be easily suppressed by putting

$$I_{\alpha, \beta, \gamma}^m = \sum_{j=0}^{\alpha} (-1)^j \binom{\alpha}{j} r_1^{2(\alpha-j)} I_{0, \beta, \gamma}^{m+2j} \quad (41.0)$$

Further, the nature of our problem is such that β can assume values of odd integers only.¹⁷ Thus the character of (39) depends on whether γ is odd or even. If it is zero or an even integer, (39) can be solved in terms of circular and algebraic functions by elementary methods.

If, however, γ is odd, (39) becomes an elliptic integral. In order to solve it we change over to a new variable

$$t = x - h, \quad (42.0)$$

where h is a constant defined so as to render

$$[r_2^2 - (\delta - x)^2][s - x] = (t - e_1)(t - e_2)(t - e_3), \quad (43)$$

subject to conditions that

$$e_1 > e_2 > e_3 \quad \text{and} \quad e_1 + e_2 + e_3 = 0.$$

Evidently

$$h = \frac{1}{3}(2\delta + s), \quad (44)$$

and

$$\left. \begin{aligned} e_1 &= +\frac{1}{3}(\delta - s) + r_2, \\ e_2 &= -\frac{2}{3}(\delta - s), \\ e_3 &= +\frac{1}{3}(\delta - s) - r_2, \end{aligned} \right\} \quad (45.0)$$

if the eclipse is partial, and

$$\left. \begin{aligned} e_1 &= -\frac{2}{3}(\delta - s), \\ e_2 &= +\frac{1}{3}(\delta - s) + r_2, \\ e_3 &= +\frac{1}{3}(\delta - s) - r_2, \end{aligned} \right\} \quad (45.1)$$

if it is annular. In either case we are therefore entitled to put

$$t = \wp(u), \quad (42.1)$$

where \wp denotes the Weierstrass π -function of an argument u which replaces t as our independent variable.

The integrals on the right-hand side of (41.0) in terms of this new variable become

$$I_{0, \beta, \gamma}^m = -2i^{\beta+\gamma}(2\delta)^{\gamma/2} \int_{\omega_2}^{\omega_1+\omega_2} \{\wp(u) - e_1\}[\wp(u) - e_3]^{\beta+1/2} \{\wp(u) - e_2\}^{\gamma+1/2} \{\wp(u) + h\}^m du, \quad (46.0)$$

with limits defined by

$$\left. \begin{aligned} \wp(\omega_1) &= e_1, \\ \wp(\omega_2) &= e_3. \end{aligned} \right\} \quad (47)$$

If, as in equations (38.0) or (38.1), $\beta = 1$, then (46.0) can undergo further reduction. For, by definition, we have

$$2\sqrt{[\wp(u) - e_1][\wp(u) - e_2][\wp(u) - e_3]} = \wp'(u), \quad (48)$$

where accent denotes derivative with respect to u . Squaring (48) and inserting in (46.0) we obtain

$$I_{0, 1, \gamma}^m = -\frac{i^{\gamma+1}}{2}(2\delta)^{\gamma/2} \int_{\omega_2}^{\omega_1+\omega_2} [\wp(u) - e_2]^{\gamma-1/2} [\wp(u) + h]^m [\wp'(u)]^2 du. \quad (46.1)$$

¹⁷ Terms with β zero or an even integer do not occur in the light curve on account of symmetry.

But, if we abbreviate

$$\begin{aligned} g_2 &= -4(e_1e_2 + e_1e_3 + e_2e_3), \\ g_3 &= +4e_1e_2e_3, \end{aligned} \quad (49)$$

it follows from (48) that¹⁸

$$\{\varphi'(u)\}^2 = 4\varphi^3(u) - g_2\varphi(u) - g_3 \quad (50)$$

and hence, γ being odd, the whole integrand of (46.1) can be written out as a polynomial of the $\frac{1}{2}(\gamma - 1) + m + 3$ th degree in powers of $\varphi(u)$.

The last step in the evaluation of (46.0) or (46.1) consists in reducing integrals

$$\int_{\omega_2}^{\omega_1 + \omega_2} \{\varphi(u)\}^j du, \quad j = 0, 1, 2, \dots \quad (A)$$

to Legendre normal forms. This can proceed by expressing, by successive differentiation of (50), the powers of $\varphi(u)$ in terms of its derivatives. A general expression for $\varphi^j(u)$ contains, in addition to $\varphi^{11(j-1)}(u)$ and lower derivatives of even orders, also the first power of $\varphi(u)$ (for $j > 2$) and a constant. If we put

$$\int_{\omega_2}^{\omega_1 + \omega_2} du = \omega_1 \quad \text{and} \quad \int_{\omega_2}^{\omega_1 + \omega_2} \varphi(u) du = -\eta_1$$

and remember that odd derivatives of $\varphi(u)$ with arguments $\omega_1 + \omega_2$ or ω_2 vanish, we readily see¹⁹ that

$$\int_{\omega_2}^{\omega_1 + \omega_2} \{\varphi(u)\}^2 du = \frac{1}{12} g_2 \omega_1$$

and for $j > 2$ all integrals of powers of $\varphi(u)$ can be expressed as a linear combinations of ω_1 and η_1 , with coefficients involving powers and cross-products of the invariants g_2 and g_3 . The functions ω_1 and η_1 rewritten in terms of Legendre normal integrals take finally the forms

$$\omega_1 = \frac{F\left(\frac{\pi}{2}, \kappa\right)}{\sqrt{e_1 - e_3}} \quad (51)$$

and

$$\eta_1 = \sqrt{e_1 - e_3} E\left(\frac{\pi}{2}, \kappa\right) - \frac{e_1}{\sqrt{e_1 - e_3}} F\left(\frac{\pi}{2}, \kappa\right), \quad (52)$$

where F and E denote the Legendre complete integrals of the first and second kind, with the modulus

$$\kappa^2 = \frac{e_2 - e_3}{e_1 - e_3}. \quad (53)$$

The reader should notice that the moduli appropriate for partial and annular eclipses are mutually reciprocal.

11. After having thus established the solution of (39) in a finite number of terms for any value of the subscripts and of m , let us return to (40). Integrating II by parts we obtain

$$\Pi_{2r}^m = GD_{2r}^m(s) - \sqrt{\frac{\delta}{2}} \int_{c_3}^{c_2} \frac{XD_{2r}^m(x) dx}{\sqrt{(x - c_1)(x - c_2)(x - c_3)}}, \quad (54)$$

¹⁸ This is the differential equation defining $\varphi(u)$; cf. Whittaker and Watson, *Modern Analysis*, Cambridge, 1920, sec. 20.22.

¹⁹ Cf. *op. cit.*, sec. 20.52.

where $G = \frac{\pi}{2}$ or 0 as to whether the eclipse is partial or annular, X stands for

$$\frac{x^2 - 2sx + r_1^2}{r_1^2 - x^2},$$

and

$$c_1 = \delta + r_2,$$

$$c_2 = s,$$

$$c_3 = \delta - r_2,$$

if the eclipse is partial, and

$$c_1 = s,$$

$$c_2 = \delta + r_2,$$

$$c_3 = \delta - r_2,$$

if it is annular. Substitute, as before,

$$x - \frac{1}{3} \sum_{j=1}^3 c_j = \wp(u) \quad (42.0)$$

and expand

$$XD_{2r}^m(x) = \sum_{j=0}^{m+n+2} a_n^m(j) \{\wp(u)\}^j + b_n^m r_1^{m+n+2} \left\{ \frac{r_1 - s}{\wp(u) + h - r_1} + (-1)^m \frac{r_1 + s}{\wp(u) + h + r_1} \right\},$$

where the coefficients a_n^m are polynomials of the $(m+n+2-j)$ th degree in r_1 , δ , and s , and b_n^m is a positive fraction (numerical factor). Since, by definition,

$$dx = 2\sqrt{(x - c_1)(x - c_2)(x - c_3)} du \quad (48)$$

we see that the Π_{2r}^m can be expressed in terms of integrals of powers of $\wp(u)$ which we have just solved, plus two integrals of the form

$$\int_{\omega_1}^{\omega_1 + \omega_2} \frac{du}{\wp(u) + h \pm r_1}, \quad (B)$$

which are new and remain to be evaluated.

In order to do so we introduce new arguments $v_{1,2}$ defined by

$$-(h \pm r_1) = \wp(v_{1,2}). \quad (55.00)$$

Then, by means of a well-known theorem²⁰ we have

$$\int_{\omega_1}^{\omega_1 + \omega_2} \frac{du}{\wp(u) - \wp(v_j)} = \frac{2}{\wp'(v_j)} \{\omega_1 \zeta(v_j) - \eta_j v_j\}, \quad j = 1, 2, \quad (56)$$

where accent denotes derivative with respect to v_j and ζ is the Weierstrass zeta-function. As one can easily verify,

$$\wp'(v_{1,2}) = \mp 2i\sqrt{2\delta}(r_1 \pm s) \quad (55.10)$$

if the eclipse is partial, and

$$\wp'(v_{1,2}) = -2i\sqrt{2\delta}(r_1 \pm s) \quad (55.11)$$

if it is annular. In order to remove the imaginary unit we put

$$\begin{aligned} v_1 &= iw_1, \\ v_2 &= iw_2 + \omega_1. \end{aligned} \quad (57)$$

Remembering that

$$\zeta(\omega_1) = \eta_1, \quad \wp(\omega_1) = e_1, \quad \wp'(\omega_1) = 0,$$

²⁰ Whittaker and Watson, *op. cit.*, sec. 20.53.

the addition-theorem for Weierstrass zeta-functions yields

$$\zeta(\omega_1 + iw_j) = \eta_1 + \zeta(iw_j) + \frac{i}{\sqrt{2\delta}} \{r_1 - (\delta - r_2)\}$$

if the eclipse is partial, and

$$\zeta(\omega_1 + iw_j) = \eta_1 + \zeta(iw_j) + i\sqrt{2\delta}$$

if it is annular. If we further substitute

$$\zeta(iw) = -i\zeta^*(w), \quad (58)$$

where

$$\zeta^*(w; e_1, e_2, e_3) = \zeta(w; -e_1, -e_2, -e_3),$$

we finally obtain that, for partial eclipses,

$$\sqrt{2\delta}(r_1 + s) \int_{\omega_2}^{\omega_1 + \omega_2} \frac{du}{\wp(u) - \wp(v_1)} = \omega_1 \zeta^*(w_1) + \eta_1 w_1, \quad (59.0)$$

and

$$\sqrt{2\delta}(r_1 - s) \int_{\omega_2}^{\omega_1 + \omega_2} \frac{du}{\wp(u) - \wp(v_2)} = -\omega_1 \zeta^*(w_2) - \eta_1 w_2 + \frac{\omega_1}{\sqrt{2\delta}} (r_1 + r_2 - \delta). \quad (59.10)$$

If the eclipse is annular, equation (59.0) continues to hold good; but (59.10) is to be replaced by

$$\sqrt{2\delta}(r_1 - s) \int_{\omega_2}^{\omega_1 + \omega_2} \frac{du}{\wp(u) - \wp(v_2)} = \omega_1 \zeta^*(w_2) + \eta_1 w_2 - \omega_1 \sqrt{2\delta}. \quad (59.11)$$

The functions $w_{1,2}$ and $\zeta^*(w_{1,2})$, expressed in terms of Legendre normal forms, become

$$w_{1,2} = \frac{F(\phi_{1,2}, \kappa')}{\sqrt{e_1 - e_3}} \quad (60)$$

and

$$(p) \quad \zeta^*(w_{1,2}) = e_3 w_{1,2} + \sqrt{e_1 - e_3} E(\phi_{1,2}, \kappa') + \frac{1}{\sqrt{2\delta}} [r_1 \pm (\delta - r_2)], \quad (61.0)$$

$$(a) \quad \zeta^*(w_{1,2}) = e_3 w_{1,2} + \sqrt{e_1 - e_3} E(\phi_{1,2}, \kappa') + \sqrt{2\delta}, \quad (61.1)$$

—as to whether the eclipse is partial (*p*) or annular (*a*)—where κ' , the complementary modulus, is defined by

$$(\kappa')^2 = \frac{e_1 - e_2}{e_1 - e_3} = 1 - \kappa^2, \quad (62)$$

and the amplitudes for partial and annular eclipses take the respective forms

$$(p) \quad \phi_1 = \sin^{-1} \sqrt{\frac{2r_2}{r_1 + r_2 + \delta}}, \quad \phi_2 = \sin^{-1} \sqrt{\frac{2\delta}{r_1 + r_2 + \delta}}, \quad (63.0)$$

and

$$(a) \quad \phi_1 = \phi_2 = \sin^{-1} \sqrt{\frac{r_1 + r_2 - \delta}{r_1 + r_2 + \delta}}. \quad (63.1)$$

Let us put, for brevity's sake,

$$(r_1 + s) \int_{\omega_2}^{\omega_1 + \omega_2} \frac{du}{\wp(u) - \wp(v_1)} \mp (r_1 - s) \int_{\omega_2}^{\omega_1 + \omega_2} \frac{du}{\wp(u) - \wp(v_2)} = \frac{1}{\sqrt{2\delta}} \mathfrak{E}_{1,2}. \quad (64)$$

By combination of the above formulae it follows that, for partial eclipses,

$$\mathfrak{G}_{1,2} = \left\{ E\left(\frac{\pi}{2}, \kappa\right) - F\left(\frac{\pi}{2}, \kappa\right) \right\} \left\{ F(\phi_1, \kappa') \pm F(\phi_2, \kappa') \right\} + F\left(\frac{\pi}{2}, \kappa\right) \left\{ E(\phi_1, \kappa') \pm E(\phi_2, \kappa') + \kappa \cos \phi_1 \sec \phi_2 \right\}. \quad (65.00)$$

If the upper sign is valid, this expression admits of a drastic simplification; for, by an obvious extension of a theorem due to Legendre,²¹ the reader should have no difficulty to prove that

$$\mathfrak{G}_1 = \frac{\pi}{2} + \sqrt{\frac{\delta}{r_2}} F\left(\frac{\pi}{2}, \kappa\right). \quad (65.10)$$

Hence, by subtraction of \mathfrak{G}_1 and \mathfrak{G}_2 , the latter takes the form

$$\mathfrak{G}_2 = \frac{\pi}{2} - 2 \left\{ E\left(\frac{\pi}{2}, \kappa\right) - F\left(\frac{\pi}{2}, \kappa\right) \right\} F(\phi_2, \kappa') - 2 \left\{ E(\phi_2, \kappa') - \frac{1}{2} \sqrt{\frac{\delta}{r_2}} \right\} F\left(\frac{\pi}{2}, \kappa\right), \quad (65.2)$$

in which both kinds of incomplete integrals possess a common amplitude.

If, finally, the eclipse is annular we similarly obtain

$$\mathfrak{G}_1 = \kappa \sqrt{\frac{\delta}{r_2}} F\left(\frac{\pi}{2}, \kappa\right), \quad (65.11)$$

and

$$\mathfrak{G}_2 = 2F(\phi_{1,2}, \kappa') \left\{ E\left(\frac{\pi}{2}, \kappa\right) - F\left(\frac{\pi}{2}, \kappa\right) \right\} + 2F\left(\frac{\pi}{2}, \kappa\right) \left\{ E(\phi_{1,2}, \kappa') + \frac{\kappa}{2} \sqrt{\frac{\delta}{r_2}} \right\}. \quad (65.3)$$

12. The evaluation of circular integrals associated with effects of the tidal distortion has thus been completed. We found that the expressions for \mathfrak{A}_n^m are all elementary, while those for \mathfrak{B}_n^m are such only if n is zero or an even integer. If it is odd the \mathfrak{B} 's are found to involve elliptic integrals. Expressions of the form $I_{0,1,\gamma}^m$, where γ is an odd integer, or—if m is also odd— $\Pi_{2,\gamma}^m$, can all be solved in terms of Legendre complete integrals of the first and second kind. If, however, m is zero or even, the $\Pi_{2,\gamma}^m$'s involve also complete elliptic integrals of the third kind which belong to the "circular" class and are therefore expressible in terms of incomplete integrals of the first and second kind with complementary moduli.

The second-harmonic rotational distortion invokes, in addition to terms already treated, new terms involving powers of y (cf. sec. III). Terms containing odd powers of y vanish, however, on account of symmetry, while even powers of y can always be expressed in terms of those of x and z by means of the relation $x^2 + y^2 + z^2 = r_1^2$. Hence the effects of the rotational distortion (as well as the boundary corrections) can be expressed in terms of functions already treated, and the solution of our problem is thus complete.

V. THEORETICAL LIGHT CURVES

13. The equations governing the changes of light due to eclipses in close binary systems can now be put down at once. Let us start from

$$\Delta \mathfrak{Q} = \frac{3(1-u)}{3-u} \Delta \mathfrak{Q}^U + \frac{2u}{3-u} \Delta \mathfrak{Q}^D, \quad (17.0)$$

where u is the coefficient of limb-darkening of the eclipsed star, and put

$$\Delta \mathfrak{Q}^U = \alpha^U + f_*^U + f_1^U + f_2^U, \quad (66.0)$$

$$\Delta \mathfrak{Q}^D = \alpha^D + f_*^D + f_1^D + f_2^D, \quad (66.1)$$

where α^U and α^D denote the "uniform" and "completely darkened" fractional losses of light that

²¹ Cf. Whittaker and Watson, *op. cit.*, sec. 22.735.

would take place if the eclipsed components were spherical, and the f 's represent the effects of distortion: f_* will denote effects (mainly of gravity-darkening) associated with circular integrals and expressible in terms of associated α -functions, while f_1 and f_2 stand for the boundary corrections due to the distortion of the primary (eclipsed) and secondary (eclipsing) component, respectively.

Evidently

$$\alpha^U = \alpha_0^0 \quad \text{and} \quad \alpha^D = \frac{3}{2}\alpha_1^0;$$

while by making use of equations (18.0) and (18.1), the f_* 's result as follows:

$$\begin{aligned} f_*^U = \frac{1}{3} v_1^{(2)} & \left\{ \frac{1}{2} \Omega_2^U [3(n_0^2 - n_1^2)\alpha_2^0 + 3(n_2^2 - n_1^2)\alpha_0^2 + 6n_0n_2\alpha_1^1 + 2P_2(n_1)\alpha_0^0] \right. \\ & + 2P_2(n_0)\alpha_0^0 + 3n_0n_2\alpha_{-1}^1 \Big\} \\ & - w_1^{(2)} \left\{ \frac{1}{2} \Omega_2^U [3l_0^2\alpha_2^0 + 6l_0l_2\alpha_1^1 + 3l_2^2\alpha_0^2 - \alpha_0^0] + 2P_2(l_0)\alpha_0^0 + 3l_0l_2\alpha_{-1}^1 \right\} \\ & - w_1^{(3)} \left\{ \frac{1}{2} \Omega_3^U [5l_0^3\alpha_3^0 + 15l_0^2l_2\alpha_2^1 + 15l_0l_2^2\alpha_1^2 + 5l_2^3\alpha_0^3 - 3l_0\alpha_1^0 - 3l_2\alpha_0^1] \right. \\ & + [l_0\alpha_1^0 + 2l_2\alpha_0^1]P_3'(l_0) - \frac{3}{2}\alpha_1^0 + \frac{3}{2}l_0[5l_2^2\alpha_{-1}^2 - l_0\alpha_{-1}^0] \Big\} \\ & - w_1^{(4)} \left\{ \frac{1}{8} \Omega_4^U [35l_0^4\alpha_4^0 + 140l_0^3l_2\alpha_3^1 + 210l_0^2l_2^2\alpha_2^2 + 140l_0l_2^3\alpha_1^3 \right. \\ & + 35l_2^4\alpha_0^4 - 30l_0^2\alpha_2^0 - 60l_0l_2\alpha_1^1 - 30l_2^2\alpha_0^2 + 3\alpha_0^0] \\ & + l_0P_4'(l_0)\alpha_2^0 + \frac{15}{2}l_2^2(7l_0^2 - 1)\alpha_0^2 - P_3'(l_0)\alpha_0^0 \\ & + \frac{5}{2}l_0l_2[3(7l_0^2 - 2)\alpha_1^1 + 7l_2^2\alpha_{-1}^1 - 3\alpha_{-1}^0] \Big\} + \dots \end{aligned} \quad (67.0)$$

and

$$\begin{aligned} f_*^D = \frac{1}{2} v_1^{(2)} & \left\{ \frac{1}{2} \Omega_2^D [3(n_0^2 - n_1^2)\alpha_3^0 + 3(n_2^2 - n_1^2)\alpha_1^2 + 6n_0n_2\alpha_2^1 + 2P_2(n_1)\alpha_1^0] \right. \\ & + 4P_2(n_0)\alpha_1^0 + 6n_0n_2\alpha_0^1 \Big\} \\ & - \frac{3}{2} w_1^{(2)} \left\{ \frac{1}{2} \Omega_2^D [3l_0^2\alpha_3^0 + 6l_0l_2\alpha_2^1 + 3l_2^2\alpha_1^2 - \alpha_1^0] + 4P_2(l_0)\alpha_1^0 + 6l_0l_2\alpha_0^1 \right\} \\ & - \frac{3}{2} w_1^{(3)} \left\{ \frac{1}{2} \Omega_3^D [5l_0^3\alpha_4^0 + 15l_0^2l_2\alpha_3^1 + 15l_0l_2^2\alpha_2^2 + 5l_2^3\alpha_1^3 - 3l_0\alpha_2^0 - 3l_2\alpha_1^1] \right. \\ & + 2[l_0\alpha_2^0 + 2l_2\alpha_1^1]P_3'(l_0) + 3[5l_0l_2^2\alpha_0^2 - l_0^2\alpha_0^0 - \alpha_2^0] \Big\} \\ & - \frac{3}{2} w_1^{(4)} \left\{ \frac{1}{8} \Omega_4^D [35l_0^4\alpha_5^0 + 140l_0^3l_2\alpha_4^1 + 210l_0^2l_2^2\alpha_3^2 + 140l_0l_2^3\alpha_2^3 + 35l_2^4\alpha_1^4 - 30l_0^2\alpha_3^0 \right. \\ & - 60l_0l_2\alpha_2^1 - 30l_2^2\alpha_1^2 + 3\alpha_1^0] + 2l_0P_4'(l_0)\alpha_3^0 + 15l_2^2(7l_0^2 - 1)\alpha_1^2 - 2P_3'(l_0)\alpha_1^0 \\ & + 5l_0l_2[3(7l_0^2 - 2)\alpha_2^1 + 7l_2^2\alpha_0^3 - 3\alpha_0^1] \Big\} + \dots, \end{aligned} \quad (67.1)$$

where

$$\Omega_j^U = \left\{ \left(\frac{2j+1}{\Delta_j} + 1 - j \right) \tau - j - 2 \right\}; \quad \Omega_j^D = \Omega_j^U - j. \quad (68)$$

The boundary corrections f_1 , arising from the distortion of the primary component, can readily be expressed in terms of integrals of the form $I_{2\alpha, \beta, \gamma}^m$ discussed already in section IV in connection with

the associated α -functions. If we combine equations (27), (28), and (33) and put, for brevity's sake,

$$(r_2^2 - \delta^2)I_{0,\beta,\gamma}^m + \delta I_{0,\beta,\gamma}^{m+1} = \pi r_1^2 \mathfrak{Z}_{\beta,\gamma}^m, \quad (69)$$

where

$$q = 3 + \beta + \gamma + m,$$

then

$$\begin{aligned} f_1^U = & \frac{1}{3} v_1^{(2)} \left\{ 3n_0^2 \mathfrak{Z}_{-1,2}^0 + 3n_1^2 \mathfrak{Z}_{-1,0}^0 + 3n_2^2 \mathfrak{Z}_{-1,0}^2 + 6n_0 n_2 \mathfrak{Z}_{-1,1}^1 - \mathfrak{Z}_{-1,0}^0 \right\} \\ & - w_1^{(2)} \left\{ 3l_0^2 \mathfrak{Z}_{-1,2}^0 + 6l_0 l_2 \mathfrak{Z}_{-1,1}^1 + 3l_2^2 \mathfrak{Z}_{-1,0}^2 - \mathfrak{Z}_{-1,0}^0 \right\} \\ & - w_1^{(3)} \left\{ 5l_0^3 \mathfrak{Z}_{-1,3}^0 + 15l_0^2 l_2 \mathfrak{Z}_{-1,2}^1 + 15l_0 l_2^2 \mathfrak{Z}_{-1,1}^2 + 5l_2^3 \mathfrak{Z}_{-1,0}^3 - 3l_0 \mathfrak{Z}_{-1,1}^0 - 3l_2 \mathfrak{Z}_{-1,0}^1 \right\} \\ & - \frac{1}{4} w_1^{(4)} \left\{ 35l_0^4 \mathfrak{Z}_{-1,4}^0 + 140l_0^3 l_2 \mathfrak{Z}_{-1,3}^1 + 210l_0^2 l_2^2 \mathfrak{Z}_{-1,2}^2 + 140l_0 l_2^3 \mathfrak{Z}_{-1,1}^3 + 35l_2^4 \mathfrak{Z}_{-1,0}^4 \right. \\ & \left. - 30l_2^2 \mathfrak{Z}_{-1,2}^0 - 60l_0 l_2 \mathfrak{Z}_{-1,1}^1 - 30l_2^2 \mathfrak{Z}_{-1,0}^2 + 3\mathfrak{Z}_{-1,0}^0 \right\} + \dots \end{aligned} \quad (70.0)$$

and

$$\begin{aligned} f_1^D = & \frac{1}{2} v_1^{(2)} \{ 3n_0^2 \mathfrak{Z}_{-1,3}^0 + 3n_1^2 \mathfrak{Z}_{-1,1}^0 + 3n_2^2 \mathfrak{Z}_{-1,1}^2 + 6n_0 n_2 \mathfrak{Z}_{-1,2}^1 - \mathfrak{Z}_{-1,1}^0 \} \\ & - \frac{3}{2} w_1^{(2)} \{ 3l_0^2 \mathfrak{Z}_{-1,3}^0 + 6l_0 l_2 \mathfrak{Z}_{-1,2}^1 + 3l_2^2 \mathfrak{Z}_{-1,1}^2 - \mathfrak{Z}_{-1,1}^0 \} \\ & - \frac{3}{2} w_1^{(3)} \{ 5l_0^3 \mathfrak{Z}_{-1,4}^0 + 15l_0^2 l_2 \mathfrak{Z}_{-1,3}^1 + 15l_0 l_2^2 \mathfrak{Z}_{-1,2}^2 + 5l_2^3 \mathfrak{Z}_{-1,1}^3 - 3l_0 \mathfrak{Z}_{-1,2}^0 - 3l_2 \mathfrak{Z}_{-1,1}^1 \} \\ & - \frac{3}{8} w_1^{(4)} \{ 35l_0^4 \mathfrak{Z}_{-1,5}^0 + 140l_0^3 l_2 \mathfrak{Z}_{-1,4}^1 + 210l_0^2 l_2^2 \mathfrak{Z}_{-1,3}^2 + 140l_0 l_2^3 \mathfrak{Z}_{-1,2}^3 + 35l_2^4 \mathfrak{Z}_{-1,1}^4 \\ & - 30l_0^2 \mathfrak{Z}_{-1,3}^0 - 60l_0 l_2 \mathfrak{Z}_{-1,2}^1 - 30l_2^2 \mathfrak{Z}_{-1,1}^2 + 3\mathfrak{Z}_{-1,1}^0 \} + \dots \end{aligned} \quad (70.1)$$

The remaining part of the boundary corrections arising from the distortion of the shadow cylinder cast by the secondary (eclipsing) component follows similarly. Combining equations (30), (31), and (33) we obtain

$$\begin{aligned} (r_1/r_2)^2 f_2^U = & -\frac{1}{3} v_2^{(2)} \{ 3n_1^2 I_{-1,0}^0 + 3n_2^2 I_{-1,0}^2 - I_{-1,0}^0 \} \\ & + w_2^{(2)} \{ 3l_2^2 I_{-1,0}^2 - I_{-1,0}^0 \} + w_2^{(3)} \{ 5l_2^3 I_{-1,0}^3 - 3l_2 I_{-1,0}^1 \} \\ & + \frac{1}{4} w_2^{(4)} \{ 35l_2^4 I_{-1,0}^4 - 30l_2^2 I_{-1,0}^2 + 3I_{-1,0}^0 \}, \end{aligned} \quad (71.0)$$

and

$$\begin{aligned} (r_1/r_2)^2 f_2^D = & -\frac{1}{2} v_2^{(2)} \{ 3n_1^2 I_{-1,1}^0 + 3n_2^2 I_{-1,1}^2 - I_{-1,1}^0 \} \\ & + \frac{3}{2} w_2^{(2)} \{ 3l_2^2 I_{-1,1}^2 - I_{-1,1}^0 \} + \frac{3}{2} w_2^{(3)} \{ 5l_2^3 I_{-1,1}^3 - 3l_2 I_{-1,1}^1 \} \\ & + \frac{3}{8} w_2^{(4)} \{ 35l_2^4 I_{-1,1}^4 - 30l_2^2 I_{-1,1}^2 + 3I_{-1,1}^0 \}, \end{aligned} \quad (71.1)$$

where

$$\pi r_2^{q-2} I_{\beta,\gamma}^m = \int_{\alpha}^{\alpha} [r_2^2 - (\delta - x)^2]^{\beta/2} [2\delta(s - x)]^{\gamma/2} [\delta - x]^m dx. \quad (72)$$

14. If the component undergoing eclipse happens to be the smaller of the two, then for $\delta = r_2 - r_1$ the eclipse becomes total and the loss of light equals the luminosity of the primary star. In such a case the foregoing algebra admits of drastic simplification. The boundary corrections evidently vanish, and so do the \mathfrak{B}_n^m 's of the circular integrals; while the normalized \mathfrak{A}_n^m 's degenerate for $s = r_1$ into numerical factors. The fractional luminosity \mathfrak{L}_1 of the distorted primary star then takes the form

$$\begin{aligned} \mathfrak{L}_1 = 1 + \frac{3(1-u)}{3-u} \left\{ \frac{1}{3} v_1^{(2)} \left[1 + \frac{\tau}{4} \left(\frac{5}{\Delta_2} - 1 \right) \right] P_2(n_0) - w_1^{(2)} \left[1 + \frac{\tau}{4} \left(\frac{5}{\Delta_2} - 1 \right) \right] P_2(l_0) \right. \\ \left. + \frac{3}{4} w_1^{(4)} \left[1 + \frac{\tau}{18} \left(\frac{9}{\Delta_4} - 3 \right) \right] P_4(l_0) + \dots \right\} \\ + \frac{2u}{3-u} \left\{ \frac{8}{15} v_1^{(2)} \left[1 + \frac{\tau}{4} \left(\frac{5}{\Delta_2} - 1 \right) \right] P_2(n_0) - \frac{8}{5} w_1^{(2)} \left[1 + \frac{\tau}{4} \left(\frac{5}{\Delta_2} - 1 \right) \right] P_2(l_0) \right. \\ \left. - \frac{5}{4} w_1^{(3)} \left[1 + \frac{\tau}{10} \left(\frac{7}{\Delta_3} - 2 \right) \right] P_3(l_0) + \dots \right\}, \end{aligned} \quad (73)$$

the primary's luminosity in its undistorted state being taken as the unity of light.

Equation (73) specifies evidently the variation of light of a distorted star between eclipses. We notice that no light variation arises from the third harmonic unless there is some limb-darkening, nor any from the fourth unless the limb-darkening is incomplete. These particular properties of the even and odd harmonics higher than the second were already pointed out by Russell²² in an early paper on the light variation of asteroids. We further notice that the effect of gravity-darkening, upon variation of total light between eclipses, arising from the second, third, and fourth tidal harmonic distortion of a centrally condensed star, is in general to multiply the variation invoked by the distorted geometry alone by the factors of 2, $\frac{3}{2}$, and $\frac{4}{3}$, respectively. These results are not wholly new. Equation similar to (73) for the special case of centrally condensed stars and total radiation has first been derived by Takeda,²³ and later generalized by Sterne²⁴ for stars of any structure with an arbitrary coefficient of gravity-darkening. The variation of light caused by the changing geometry alone, with coefficient of gravity-darkening appropriate for black-body radiation, were to the same order of accuracy deduced first by the writer.²⁵

15. Within minima, however, the changes of light due to the eclipse of a rotationally and tidally distorted star become vastly more complex, and equations (67), (70), and (71) then represent a general and rigorous solution of the problem set forth in the introduction of the present paper. As it could have been anticipated, its form is by no means simple. In particular, effects of the second, third, and fourth spherical harmonic distortion invoke, in addition to the two fundamental modes α_0^0 and α_1^0 , 22 further associated α -functions of various orders and indices summarized in the following scheme,

$$\begin{array}{ccccccc} \alpha_{-1}^0 & \alpha_{-1}^1 & \alpha_{-1}^2 & \alpha_{-1}^3 & & & \\ & \alpha_0^1 & \alpha_0^2 & \alpha_0^3 & \alpha_0^4 & & \\ & \alpha_1^1 & \alpha_1^2 & \alpha_1^3 & \alpha_1^4 & & \\ \alpha_2^0 & \alpha_2^1 & \alpha_2^2 & \alpha_2^3 & & & \\ \alpha_3^0 & \alpha_3^1 & \alpha_3^2 & & & & \\ \alpha_4^0 & \alpha_4^1 & & & & & \\ \alpha_5^0 & & & & & & \end{array}$$

plus an analogous number of functions of the type $\mathfrak{B}_{\beta,\gamma}^m$ and $I_{\beta,\gamma}^m$. All these functions have been defined and their properties investigated in section IV, so that the task which remains is to evaluate them explicitly in a finite number of terms.

²² *Ap.J.*, 24, 1, 1906.

²³ *Kyoto Mem.*, A, 17, 197, 1934.

²⁴ *Proc. Nat. Acad. Sci.*, 27, 99, 1941.

²⁵ *Ann. New York Acad. Sci.*, 41, 13, 1941.

VI. EVALUATION OF THE INTEGRALS

16. As to the associated α -functions, in section IV we found that their character depends substantially on whether their index n is odd or even. If it is zero or an even integer, the associated α -functions assume the form

$$\pi^2 r_1^{m+2(\nu+1)} \alpha_{2\nu}^m = B(\frac{1}{2}, \nu + 1) \{ 2G[D_{2\nu+1}^m(r_1) - D_{2\nu+1}^m(s)] + \sum_{j=0}^{\nu} B(\frac{1}{2}, \frac{1}{2} + \nu - j) I_{2j, 1, 2(\nu-j)}^m \}, \quad (74.0)$$

where $G = \pi/2$ or 0 as to whether the eclipse is partial or annular; while if the index is odd,

$$\pi^2 r_1^{m+2\nu+1} \alpha_{2\nu-1}^m = 2B(\frac{1}{2}, \frac{1}{2} + \nu) \left\{ GD_{2\nu}^m(r_1) + \frac{1}{2} \sum_{j=1}^{\nu} B(\frac{1}{2}, j) I_{2j-1, 1, 2j-1}^m - \sqrt{\frac{\delta}{2}} \int_{c_1}^{c_2} \frac{XD_{2\nu}^m(x)dx}{\sqrt{(x-c_1)(x-c_2)(x-c_3)}} \right\}. \quad (74.1)$$

Functions of the former kind can be evaluated in terms of circular and algebraic functions, while those of the latter kind are expressible only by means of elliptic integrals.

Let us consider the former case first. By direct integration we easily find that, as long as the eclipse is partial,

$$\pi r_1^2 \alpha_0^0 = r_1^2 \cos^{-1} \frac{s}{r_1} + r_2^2 \cos^{-1} \frac{\delta - s}{r_2} - \delta \sqrt{r_1^2 - s^2} \quad (75.0)$$

and

$$\pi r_1^3 \alpha_0^1 = \delta r_2^2 \cos^{-1} \frac{\delta - s}{r_2} - \delta(\delta - s) \sqrt{r_1^2 - s^2}; \quad (75.1)$$

while the respective functions of higher orders and indices take readily the forms:

$$\alpha_0^2 = \frac{1}{4} \alpha_0^0 + \frac{1}{4} (5D - 2S) \alpha_0^1 - \frac{5D}{6\pi} (1 - S^2)^{\frac{1}{2}}, \quad (75.2)$$

$$\alpha_0^3 = + \frac{1}{4} (7D^2 - 6DS + 3) \alpha_0^1 - \frac{D}{6\pi} (7D + S) (1 - S^2)^{\frac{1}{2}}, \quad (75.3)$$

$$\begin{aligned} \alpha_0^4 = & \frac{1}{8} \alpha_0^0 + \frac{1}{8} \{ 7D^2(3D - 4S) + 2(7D - 2S) + 4DS^2 \} \alpha_0^1 \\ & - \frac{D}{60\pi} \{ 35D(3D - S) + 6S^2 + 49 \} (1 - S^2)^{\frac{1}{2}}, \end{aligned} \quad (75.4)$$

$$\alpha_2^0 = \frac{1}{2} \alpha_0^0 - \frac{1}{2} (3D - 2S) \alpha_0^1 + \frac{D}{\pi} (1 - S^2)^{\frac{1}{2}}, \quad (76.0)$$

$$\alpha_2^1 = - 2D(D - S) \alpha_0^1 + \frac{4D^2}{3\pi} (1 - S^2)^{\frac{1}{2}}, \quad (76.1)$$

$$\begin{aligned} \alpha_2^2 = & \frac{1}{12} \alpha_0^0 - \frac{1}{12} \{ 5D^2(7D - 10S) + 2(5D - S) + 8DS^2 \} \alpha_0^1 \\ & + \frac{D}{18\pi} \{ 5D(7D - 3S) + 3 \} (1 - S^2)^{\frac{1}{2}}, \end{aligned} \quad (76.2)$$

$$\begin{aligned} \alpha_2^3 = & - \frac{D}{2} \{ D^2(9D - 17S) + 3S(2DS - 1) + 5D \} \alpha_0^1 \\ & + \frac{D^2}{15\pi} \{ D(9D - 8S) + 16 - S^2 \} (1 - S^2)^{\frac{1}{2}}, \end{aligned} \quad (76.3)$$

$$\alpha_4^0 = \frac{1}{3} \alpha_0^0 + \frac{1}{3} \{2D^2(5D - 8S) + D(4S^2 - 1) + 2S\} \alpha_0^1 - \frac{2D}{9\pi} \{2D(5D - 3S) - 3\} (1 - S^2)^{\frac{1}{2}}, \quad (77.0)$$

$$\alpha_4^1 = + \frac{D^2}{35} \{177(D - S)^2 + 37(1 - S^2) - 2D^2\} \alpha_0^1 - \frac{10D^2}{3\pi} (D - S)(1 - S^2)^{\frac{1}{2}}; \quad (77.1)$$

where we have abbreviated $\delta/r_1 = D$ and $s/r_1 = S$.

If, however, $r_1 > r_2$ and $\delta < r_1 - r_2$, the eclipse becomes annular; and the respective associated α -functions of even indices then result as follows. For $n = 0$ equation (74.0) yields

$$\pi r_1^{m+2} \alpha_0^m = 2I_{0,1,0}^m.$$

By direct integration we easily find that, during annular eclipse,

$$\alpha_0^0 = k^2, \quad (78.0)$$

$$\alpha_0^1 = k^2 D, \quad (78.1)$$

where k is the ratio of radii defined, as usual, by

$$k = r(\text{smaller})/r(\text{larger}).$$

Associated α -functions of zero index and higher orders then follow from a simple recursion formula

$$(m+2)\alpha_0^m = (2m+1)D\alpha_0^{m-1} + (m-1)(k^2 - D^2)\alpha_0^{m-2} \quad (79.0)$$

and take the forms

$$\alpha_0^2 = k^2(D^2 + \frac{1}{4}k^2), \quad (78.2)$$

$$\alpha_0^3 = k^2(D^2 + \frac{3}{4}k^2)D, \quad (78.3)$$

$$\alpha_0^4 = k^2(D^4 + \frac{3}{2}k^2D^2 + \frac{1}{8}k^4). \quad (78.3)$$

If, finally, $n = 2$ or 4 , the respective associated α -functions can be obtained by combining the preceding equations by means of the formulae

$$\alpha_2^m = \frac{2}{3} \{ (1 + DS)\alpha_0^m - D\alpha_0^{m+1} - \alpha_0^{m+2} \} \quad (79.1)$$

and

$$\alpha_4^m = \frac{4}{3} \{ \alpha_2^m + D^2\alpha_0^{m+2} + D^2S^2\alpha_0^m - 2D^2S\alpha_0^{m+1} - \frac{2}{3}[(1 + DS)\alpha_0^{m+2} + D\alpha_0^{m+3} + \alpha_0^{m+4}] \}. \quad (80)$$

17. The remaining thirteen associated α -functions of odd indices can be expressed only in terms of elliptic integrals. Let us put, for brevity's sake,

$$\pi \alpha_{2\nu-1}^{2\mu} = \frac{(-1)^\nu}{r_1^{2(\mu+\nu+1)-1}} \sqrt{\frac{\delta}{2}} \{ \mathfrak{P}_{2\nu-1}^{2\mu} \omega_1 - \mathfrak{Q}_{2\nu-1}^{2\mu} \eta_1 \} + \frac{\Gamma(\mu + \frac{1}{2})\Gamma(\nu + \frac{1}{2})}{\sqrt{\pi}\Gamma(\mu + \nu + \frac{3}{2})} \left\{ \mathfrak{E}_2 + \frac{\pi}{2} \right\} \quad (81)$$

and

$$\pi \alpha_{2\nu-1}^{2\mu+1} = \frac{(-1)^\nu}{r_1^{2(\mu+\nu+1)}} \sqrt{\frac{\delta}{2}} \{ \mathfrak{P}_{2\nu-1}^{2\mu+1} \omega_1 - \mathfrak{Q}_{2\nu-1}^{2\mu+1} \eta_1 \}, \quad (82)$$

where ω_1 , η_1 , and \mathfrak{E}_2 are given by equations (51), (52), and (65.2) or (65.3) as to whether the eclipses are partial or annular. Then, using the procedure and abbreviations of section IV, we find that for

both partial and annular eclipses the \mathfrak{P} 's and \mathfrak{Q} 's take the following forms:

$$\mathfrak{P}_{-1}^0 = 4(h - 2s), \quad (83.00)$$

$$\mathfrak{P}_{-1}^1 = \frac{8}{9}(r_1^2 + 2r_2^2 - s^2), \quad (83.01)$$

$$\mathfrak{P}_{-1}^2 = \frac{1}{3} \left\{ \frac{2}{5} g_3 + \frac{1}{3} (2h - 2s) g_2 + 4h^2(h - 2s) + 8r_1^2(h - s) \right\}, \quad (83.02)$$

$$\mathfrak{P}_{-1}^3 = \left\{ \frac{5}{336} g_2^2 + \frac{1}{5} (2h - s) g_3 + \frac{1}{6} (3h^2 - 3hs + r_1^2) g_2 + (h^2 + r_1^2)(h^2 - 2hs + r_1^2) \right\}; \quad (83.03)$$

$$\mathfrak{Q}_{-1}^0 = 4, \quad (83.10)$$

$$\mathfrak{Q}_{-1}^1 = 4(h - s), \quad (83.11)$$

$$\mathfrak{Q}_{-1}^2 = \left\{ \frac{1}{5} g_2 + \frac{4}{3} h(3h - 4s) + \frac{8}{3} r_1^2 \right\}, \quad (83.12)$$

$$\mathfrak{Q}_{-1}^3 = \left\{ \frac{1}{7} g_3 + \frac{3}{10} (2h - s) g_2 + 2(h^2 + r_1^2)(2h - s) - 4h^2 s \right\}; \quad (83.13)$$

$$\mathfrak{P}_1^0 = \frac{2}{3} \left\{ g_3 + \frac{1}{12} (2\delta - s) g_2 + h^2(h - 2s) + r_1^2(4s - h) \right\}, \quad (84.00)$$

$$\mathfrak{P}_1^1 = \frac{1}{2} \left\{ \frac{1}{16} g_2^2 + \frac{1}{5} (8h - s) g_3 + \frac{1}{2} h(h - s) g_2 + (h^2 - r_1^2)(h^2 - 2hs + r_1^2) \right\}, \quad (84.01)$$

$$\mathfrak{P}_1^2 = \frac{1}{15} \left\{ \frac{19}{20} g_2 g_3 + \frac{5}{56} (13h - 2s) g_2^2 + \frac{1}{5} (75h^2 - 24hs + r_1^2) g_3 + \frac{1}{6} (30h^3 - 36h^2 s + 3hr_1^2 + 4r_1^2 s) g_2 + 2(3h^5 - 6h^4 s + h^3 r_1^2 + 4h^2 r_1^2 s - 4hr_1^4 + 4r_1^4 s) \right\}, \quad (84.02)$$

$$\mathfrak{P}_1^3 = \frac{1}{12} \left\{ \frac{5}{112} g_2^3 + \frac{2}{5} g_3^2 + \frac{1}{15} (39h - 4s) g_2 g_3 + \frac{1}{168} (294h^2 - 100hs + 5r_1^2) g_2^2 + \frac{2}{5} (38h^3 - 20h^2 s + 2hr_1^2 + r_1^2 s) g_3 + \frac{1}{3} (15h^4 - 20h^3 s + 3h^2 r_1^2 + 3hr_1^2 s - r_1^4) g_2 + 2(2h^6 - 4h^5 s + h^4 r_1^2 + 2h^3 r_1^2 s - 2h^2 r_1^4 + 2hr_1^4 s - r_1^6) \right\}, \quad (84.03)$$

$$\mathfrak{P}_1^4 = \frac{1}{35} \left\{ \frac{67}{168} g_2^2 g_3 + \frac{25}{7392} (175h - 18s) g_2^3 + \frac{4}{11} (14h - 2s) g_3^2 + \frac{1}{10} (175h^2 - 40hs + 2r_1^2) g_2 g_3 + \frac{5}{168} (287h^3 - 150h^2 s + 15hr_1^2 + 4r_1^2 s) g_2^2 + \frac{2}{5} (140h^4 - 100h^3 s + 15h^2 r_1^2 + 8hr_1^2 s - 4r_1^4) g_3 + \frac{1}{6} (105h^5 - 150h^4 s + 30h^3 r_1^2 + 24h^2 r_1^2 s - 12hr_1^4 + 4r_1^4 s) g_2 + 2(5h^7 - 10h^6 s + 3h^5 r_1^2 + 4h^4 r_1^2 s - 4h^3 r_1^4 + 4h^2 r_1^4 s - 4hr_1^6 + 4r_1^6 s) \right\}; \quad (84.04)$$

$$\mathfrak{Q}_1^0 = \frac{4}{9} (7r_2^2 - 4r_1^2 + \delta^2), \quad (84.10)$$

$$\mathcal{Q}_1^1 = \frac{1}{2} \left\{ g_3 + \frac{1}{10} (14h - 3s)g_3 + 2(2h^3 - 3h^2s + r_1^2s) \right\}, \quad (84.11)$$

$$\mathcal{Q}_1^2 = \frac{1}{15} \left\{ \frac{27}{40} g_2^2 + \frac{12}{7} (10h - s)g_3 + \frac{3}{10} (50h^2 - 24hs + r_1^2)g_2 \right. \\ \left. + 2(15h^4 - 24h^3s + 3h^2r_1^2 + 8hr_1^2s - 4r_1^4) \right\}, \quad (84.12)$$

$$\mathcal{Q}_1^3 = \frac{1}{12} \left\{ \frac{36}{35} g_2g_3 + \frac{1}{30} (57h - 7s)g_2^2 + \frac{2}{7} (84h^2 - 20hs + r_1^2)g_3 + \frac{3}{5} (28h^3 - 20h^2s \right. \\ \left. + 2hr_1^2 + r_1^2s)g_2 + 4(6h^5 - 10h^4s + 2h^3r_1^2 + 3h^2r_1^2s - 2hr_1^4 + r_1^4s) \right\}, \quad (84.13)$$

$$\mathcal{Q}_1^4 = \frac{1}{35} \left\{ \frac{7}{32} g_2^3 + \frac{10}{7} g_3^2 + \frac{1}{154} (2051h - 174s)g_2g_3 + \frac{7}{40} (75h^2 - 20hs + r_1^2)g_2^2 \right. \\ \left. + \frac{2}{7} (385h^3 - 150h^2s + 15hr_1^2 + 4r_1^2s)g_3 + \frac{1}{10} (665h^4 - 600h^3s + 90h^2r_1^2 \right. \\ \left. + 90h^2r_1^2 + 48hr_1^2s - 12r_1^4)g_2 + 2(35h^6 - 60h^5s + 15h^4r_1^2 + 16h^3r_1^2s \right. \\ \left. - 12h^2r_1^4 + 8hr_1^4s - 4r_1^6) \right\}; \quad (84.14)$$

$$\mathcal{P}_3^0 = \frac{1}{20} \left\{ \frac{19}{20} g_2g_3 + \frac{5}{24} (7\delta + s)g_2^2 + \frac{1}{5} (75h^2 - 24hs - 60\delta e_2 - 49r_1^2)g_3 \right. \\ \left. + \frac{1}{3} (15h^3 - 18h^2s - 6hr_1^2 + 7r_1^2s)g_2 + 2(3h^5 - 6h^4s - 4h^3r_1^2 \right. \\ \left. + 14h^2r_1^2s + hr_1^4 - 16r_1^4s) \right\}, \quad (85.00)$$

$$\mathcal{P}_3^1 = \frac{1}{16} \left\{ \frac{5}{112} g_2^3 + \frac{2}{5} g_3^2 + \frac{1}{15} (38\delta + 9s)g_2g_3 + \frac{1}{84} [147h^2 - 50hs - 29r_1^2 \right. \\ \left. - 32\delta(e_2 - h)]g_2^2 + \frac{4}{5} [19h^3 - 10h^2s - h(11r_1^2 + 12\delta e_2) + 2r_1^2s]g_3 \right. \\ \left. + \frac{1}{3} (15h^4 - 20h^3s - 6h^2r_1^2 + 12hr_1^2s - r_1^4)g_2 + 4(h^6 - 2h^5s - h^4r_1^2 \right. \\ \left. + 4h^3r_1^2s - h^2r_1^4 - 2hr_1^4s + r_1^6) \right\}, \quad (85.01)$$

$$\mathcal{P}_3^2 = \frac{1}{140} \left\{ \frac{67}{56} g_2^2g_3 + \frac{25}{672} (42\delta + 11s)g_2^3 + 2(7\delta + 2s)g_3^2 \right. \\ \left. + \frac{1}{20} (1050h^2 - 240hs + 280\delta^2 - 121r_1^2)g_2g_3 \right. \\ \left. + \frac{5}{168} [861h^3 + 2(56\delta - 225s)h^2 - 4(57r_1^2 + 56\delta e_2)h + 54r_1^2s]g_2^2 \right. \\ \left. + \frac{1}{5} [840h^4 - 600h^3s - 5(63r_1^2 + 24s^2 + 84\delta e_2)h^2 + 216hr_1^2s - 19r_1^4]g_3 \right. \\ \left. + \frac{1}{6} [315h^5 - 450h^4s - 120h^3r_1^2 + 324h^2r_1^2s - 57hr_1^4 - 16r_1^4s]g_2 + 2[15h^7 \right. \\ \left. - 30h^6s - 12h^5r_1^2 + 54h^4r_1^2s - 19h^3r_1^4 - 16h^2r_1^4s + 16hr_1^6 - 16r_1^6s] \right\}; \quad (85.02)$$

$$\mathfrak{Q}_3^0 = \frac{1}{20} \left\{ \frac{27}{40} g_2^2 + 4(5\delta + s)g_3 + \frac{1}{5} (75h^2 - 36hs - 36r_1^2 - 40\delta e_2)g_2 \right. \\ \left. + 2(15h^4 - 24h^3s - 12h^2r_1^2 + 28hr_1^2s + r_1^4) \right\}, \quad (85.10)$$

$$\mathfrak{Q}_3^1 = \frac{1}{16} \left\{ \frac{36}{35} g_2g_3 + \frac{1}{5} (9\delta + 2s)g_3^2 + \frac{8}{7} [21h^2 - 5hs - 5r_1^2 - 6\delta(e_2 - h)]g_3 \right. \\ \left. + \frac{4}{5} [21h^3 - 15h^2s - h(9r_1^2 + 8\delta e_2) + 3r_1^2s]g_2 + 8[3h^5 - 5h^4s - 2h^3r_1^2 \right. \\ \left. + 6h^2r_1^2s - hr_1^4 - r_1^4s] \right\}, \quad (85.11)$$

$$\mathfrak{Q}_3^2 = \frac{1}{70} \left\{ \frac{273}{832} g_2^2 + \frac{15}{7} g_3^2 + \frac{1}{28} (504\delta + 139s)g_2g_3 + \frac{7}{240} (675h^2 - 180hs + 160\delta^2 \right. \\ \left. - 72r_1^2)g_2^2 + \frac{3}{7} [385h^3 + 10(7\delta - 15s)h^2 - 5(25r_1^2 + 28\delta e_2)h + 18r_1^2s]g_3 \right. \\ \left. + \frac{1}{20} [1995h^4 - 1800h^3s - 20(21r_1^2 + 18s^2 + 28\delta e_2)h^2 + 648hr_1^2s - 57r_1^4]g_2 \right. \\ \left. + [105h^6 - 180h^5s - 60h^4r_1^2 + 216h^3r_1^2s - 57h^2r_1^4 - 32hr_1^4s + 16r_1^6] \right\}; \quad (85.12)$$

$$\mathfrak{P}_3^0 = \frac{1}{56} \left\{ \frac{67}{168} g_2^2g_3 + \frac{25}{2016} (42\delta + 11s)g_3^2 + \frac{2}{3} (7\delta + 2s)g_3^2 + \frac{1}{30} [240h(2h + \delta) \right. \\ \left. + 252\delta^2 - 127r_1^2]g_2g_3 + \frac{1}{504} [20\delta(253h^2 - 76r_1^2) - 15h(163h^2 + 71r_1^2) \right. \\ \left. - 224\delta e_2(5h + 8\delta)]g_2^2 + \frac{1}{5} [385h^4 - 320h^2r_1^2 + 108r_1^4 - 140\delta e_2(h^2 - r_1^2) \right. \\ \left. - 8hs(25h^2 - 16r_1^2) + 224\delta^2 e_2^2]g_3 + \frac{1}{12} [105h^5 - 150h^4s - 110h^3r_1^2 + 192h^2r_1^2s \right. \\ \left. + 9hr_1^4 - 38r_1^4s]g_2 + [5h^7 - 10h^6s - 11h^5r_1^2 + 32h^4r_1^2s + 3h^3r_1^4 \right. \\ \left. - 38h^2r_1^4s + 3hr_1^6 + 32r_1^6s] \right\}; \quad (86.00)$$

$$\mathfrak{Q}_3^0 = \frac{1}{28} \left\{ \frac{7}{64} g_2^3 + \frac{5}{7} g_3^3 + \frac{1}{84} (504\delta + 139s)g_2g_3 + \frac{7}{720} [45h(11h + 8\delta) + 288\delta^2 \right. \\ \left. - 153r_1^2]g_2^2 + \frac{1}{7} [2\delta(185h^2 - 67r_1^2) - 13h(5h^2 + 13r_1^2) - 28\delta e_2(5h + 8\delta)]g_3 \right. \\ \left. + \frac{1}{60} [15h^2(161h^2 - 122r_1^2) - 72hs(25h^2 - 16r_1^2) + 447r_1^4 - 560\delta e_2(h^2 - r_1^2) \right. \\ \left. + 896\delta^2 e_2^2]g_2 + [35h^6 - 60h^5s - 55h^4r_1^2 + 128h^3r_1^2s + 9h^2r_1^4 - 76hr_1^4s + 3r_1^6] \right\}. \quad (86.10)$$

18. A synopsis of the associated α -functions required for the solution of our problem is now complete. As is evident from the preceding equations, all these functions can be made to depend on two independent parameters, and tabulated in terms of such parameters similarly as has been done for α^U and α^D . If, as usual, the ratio of the radii of both components k and the geometrical depth of the eclipse p are adopted as independent variables and defined by

$$k = \frac{r_s}{r_l} \quad \text{and} \quad p = \frac{\delta - r_l}{r_s},$$

where r_1 and r_2 are radii of the larger and the smaller component respectively, two different sets of tables of the $\alpha_n^m(k, p)$'s will have to be computed, depending on whether the eclipsed component is the larger or the smaller of the two.

As to the particular values which the associated α -functions may assume,

$$\alpha_n^m(k, 1) = 0 \quad (87.0)$$

for every value of m or n . All associated α -functions must vanish at the beginning of the eclipse. If $r_1 < r_2$ and m is odd, the respective associated α -functions vanish also at the moment of the inner contact and hence

$$\alpha_n^{2\mu+1}(k, \pm 1) = 0; \quad (87.1)$$

while if m is zero or an even integer,

$$\alpha_{2\nu}^{2\mu}(k, -1) = \frac{\nu! \Gamma(\mu + \frac{1}{2})}{\sqrt{\pi}(\mu + \nu + 1)!}, \quad (88.0)$$

$$\alpha_{2\nu-1}^{2\mu}(k, -1) = \frac{\Gamma(\mu + \frac{1}{2}) \Gamma(\nu + \frac{1}{2})}{\sqrt{\pi} \Gamma(\mu + \nu + \frac{3}{2})}, \quad (88.1)$$

as to whether the index n is odd or even.

If, on the other hand, $r_1 > r_2$, the $\alpha_n^m(k, p)$'s at the moment of internal tangency ($p = -1$) remain functions of k . In particular, the three such functions of lowest orders and indices take the forms

$$\alpha_0^0(k, -1) = k^2, \quad (89.0)$$

$$\alpha_0^1(k, -1) = k^2(1 - k), \quad (89.1)$$

$$\alpha_1^0(k, -1) = \frac{4}{3\pi} \{ \sin^{-1} \sqrt{k} + \frac{1}{3}(4k - 3)(2k + 1)\sqrt{k(1 - k)} \}. \quad (89.2)$$

If, finally, $r_1 > r_2$ and the eclipse is central ($\delta = 0$), a glance at equations (67.0) or (67.1) reveals that coefficients of all associated α -functions of superscripts other than zero vanish; while the remaining functions of zero order reduce to

$$\alpha_n^0(k, -1/k) = \frac{2}{n+2} \{ 1 - (1 - k^2)^{1/2+n} \}. \quad (90)$$

Numerically, all associated α -functions are quantities of zero order the values of which diminish in general with increasing m and n so that

$$\alpha_n^{m+1} \leq \alpha_n^m.$$

19. The boundary corrections f_1 , due to the distortion of the primary component, were found (cf. equation 69) to be expressible in terms of integrals of the form $I_{0,\beta,\gamma}^m$ given by equation (39). In our present case $\beta = -1$ throughout—except for a single rotational term with the coefficient n_1^2 where $\beta = +1$. To the order of accuracy we are working, twenty-six integrals of the form $I_{0,-1,\gamma}^m$ are required to express the boundary corrections due to the tidal distortion of the eclipsed component, while four additional integrals $I_{0,1,\gamma}^m$ are needed to account for effects of the centrifugal force.

The solution of the respective integrals has been investigated in section IV. Those with γ zero or an even integer can again be expressed in terms of circular and algebraic functions, while if γ is odd, the integrals are elliptical. As to the former kind, by direct integration we easily find that, if the eclipse is partial,

$$I_{0,-1,0}^0 = \cos^{-1} \frac{\delta - s}{r_2}, \quad (91.0)$$

$$I_{0,-1,0}^1 = \delta \cos^{-1} \frac{\delta - s}{r_2} - \sqrt{r_1^2 - s^2}, \quad (91.1)$$

and with the aid of the recursion formula

$$m I_{0,-1,0}^m = (2m - 1) \delta I_{0,-1,0}^{m-1} + (m - 1)(r_2^2 - \delta^2) I_{0,-1,0}^{m-2} - s^{m-1} \sqrt{r_1^2 - s^2}, \quad (92)$$

it follows that

$$I_{0,-1,0}^2 = \frac{1}{2} (2\delta^2 + r_2^2) I_{0,-1,0}^0 - \frac{1}{2} (3\delta + s) \sqrt{r_1^2 - s^2}, \quad (91.2)$$

$$I_{0,-1,0}^3 = \frac{\delta}{2} (2\delta^2 + 3r_2^2) I_{0,-1,0}^0 - \frac{1}{6} (11\delta^2 + 5\delta s + 2s^2 + 4r_2^2) \sqrt{r_1^2 - s^2}, \quad (91.3)$$

$$I_{0,-1,0}^4 = \frac{1}{8} (8\delta^4 + 24\delta^2 r_2^2 + 3r_2^4) I_{0,-1,0}^0 - \frac{1}{24} \{50\delta^3 + 26\delta^2 s + (55r_2^2 + 14s^2)\delta + 6s^3 + 9r_2^2 s\} \sqrt{r_1^2 - s^2}, \quad (91.4)$$

$$I_{0,-1,0}^5 = \frac{\delta}{8} (8\delta^4 + 40\delta^2 r_2^2 + 15r_2^4) I_{0,-1,0}^0 - \frac{1}{120} \{274\delta^4 + 154\delta^3 s + (607r_2^2 + 94s^2)\delta^2 + (161r_2^2 + 54s^2)\delta s + 8(4r_2^2 + 3s^2)s^2 + 64r_2^4\} \sqrt{r_1^2 - s^2}. \quad (91.5)$$

Expressions for $I_{0,-1,2}^m$ ($0 \leq m \leq 4$) and $I_{0,-1,4}^m$ ($0 \leq m \leq 2$) can be obtained as a linear combination of the preceding formulae by means of the equations

$$I_{0,-1,2}^m = 2\delta s I_{0,-1,0}^m - 2\delta I_{0,-1,0}^{m+1}, \quad (93)$$

and

$$I_{0,-1,4}^m = 4\delta^2 s^2 I_{0,-1,0}^m - 8\delta^2 s I_{0,-1,0}^{m+1} + 4\delta^2 I_{0,-1,0}^{m+2}, \quad (94)$$

which are simple and make it unnecessary to write down the eight respective expressions in full. The two elementary rotational terms take finally the forms

$$I_{0,1,0}^0 = \frac{1}{2} r_2^2 \cos^{-1} \frac{\delta - s}{r_2} - \frac{1}{2} (\delta - s) \sqrt{r_1^2 - s^2}, \quad (95.0)$$

$$I_{0,1,0}^1 = \delta I_{0,1,0}^0 - \frac{1}{3} (r_1^2 - s^2)^{\frac{1}{2}}. \quad (95.1)$$

If the eclipse is annular, the foregoing formulae simplify considerably. In particular, if $\gamma = 0$,

$$I_{0,-1,0}^0 = \pi, \quad (96.0)$$

$$I_{0,-1,0}^1 = \pi \delta, \quad (96.1)$$

and, by means of the recursion formula

$$m I_{0,-1,0}^m = (2m - 1) \delta I_{0,-1,0}^{m-1} + (m - 1) (r_2^2 - \delta^2) I_{0,-1,0}^{m-2}, \quad (97)$$

it follows that

$$I_{0,-1,0}^2 = \pi \left(\delta^2 + \frac{1}{2} r_2^2 \right), \quad (96.2)$$

$$I_{0,-1,0}^3 = \pi \left(\delta^2 + \frac{3}{2} r_2^2 \right) \delta, \quad (96.3)$$

$$I_{0,-1,0}^4 = \pi \left(\delta^4 + 3\delta^2 r_2^2 + \frac{3}{8} r_2^4 \right), \quad (96.4)$$

$$I_{0,-1,0}^5 = \pi \left(\delta^4 + 5\delta^2 r_2^2 + \frac{15}{8} r_2^4 \right) \delta. \quad (96.5)$$

Expressions of the form $I_{0,-1,2}^m$ (for $0 \leq m \leq 4$) and $I_{0,-1,4}^m$ (for $0 \leq m \leq 2$) can be obtained as linear combination of the preceding formulae by means of equations (93) and (94) which continue to hold good.

The two elementary rotational terms for annular eclipses become

$$I_{0,1,0}^0 = \frac{1}{2} \pi r_2^2 \quad (98.0)$$

and

$$I_{0,1,0}^1 = \frac{1}{2} \pi \delta r_2^2. \quad (98.1)$$

29. If γ is odd, however, equation (46.0) yields

$$I_{0,-1,\gamma}^m = -2i^{\gamma-1} (2\delta)^{\gamma/2} \int_{\omega_2}^{\omega_1+\omega_2} \{ \varphi(u) - e_2 \}^{(\gamma+1)/2} \{ \varphi(u) + h \}^m du. \quad (46.2)$$

The solution of this integral can proceed along the line investigated in section IV; there are no practicable recursion formulae to shorten the procedure and the respective expressions have to be put down in full. If $\gamma = 1$, then

$$I_{0,-1,1}^0 = -\frac{4}{3} \sqrt{\frac{\delta}{2}} \{ 2(\delta - s)\omega_1 - 3\eta_1 \}, \quad (99.0)$$

$$I_{0,-1,1}^1 = -\frac{4}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{1}{4} g_2 + 2h(\delta - s) \right\} \omega_1 + \frac{4}{3} \sqrt{\frac{\delta}{2}} \{ 4\delta - s \} \eta_1, \quad (99.1)$$

$$I_{0,-1,1}^2 = -\frac{4}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{3}{10} g_3 + \frac{1}{2} \delta g_2 + 2h^2(\delta - s) \right\} \omega_1 + \frac{4}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{9}{20} g_2 + 3h(2\delta - s) \right\} \eta_1, \quad (99.2)$$

$$I_{0,-1,1}^3 = -\frac{4}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{5}{112} g_2^2 + \frac{1}{10} (8\delta + s)g_3 + \frac{1}{4} h(4\delta - s)g_2 + 2h^2(\delta - s) \right\} \omega_1 \\ + \frac{4}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{3}{7} g_3 + \frac{3}{20} (8\delta + s)g_2 + h^2(8\delta - 5s) \right\} \eta_1, \quad (99.3)$$

$$I_{0,-1,1}^4 = -\frac{4}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{1}{10} g_2 g_3 + \frac{5}{168} (5\delta + s)g_2^2 + \frac{1}{5} h(10\delta - s)g_3 \right. \\ \left. + \frac{1}{3} h^2(5\delta - 2s)g_2 + 2h^4(\delta - s) \right\} \omega_1 \\ + \frac{4}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{7}{80} g_2^2 + \frac{2}{7} (5\delta + s)g_3 + \frac{3}{10} h(10\delta - s)g_2 + h^3(10\delta - 7s) \right\} \eta_1, \quad (99.4)$$

$$I_{0,-1,1}^5 = -\frac{4}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{45}{4928} g_2^3 + \frac{3}{55} g_3^2 + \frac{1}{10} (4\delta + s)g_2 g_3 + \frac{25}{56} \delta h g_2^2 + h^2(4\delta - s)g_3 \right. \\ \left. + \frac{5}{4} h^3(2\delta - s)g_2 + 2h^5(\delta - s) \right\} \omega_1 \\ + \frac{4}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{261}{1540} g_2 g_3 + \frac{7}{80} (4\delta + s)g_2^2 + \frac{30}{7} \delta h g_3 + \frac{3}{2} h^2(4\delta - s)g_2 + 3h^4(4\delta - 3s) \right\} \eta_1. \quad (99.5)$$

If $\gamma = 3$,

$$I_{0,-1,3}^0 = \frac{8}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{1}{4} g_2 + \frac{4}{3} (\delta - s)^2 \right\} \delta \omega_1 - \frac{32}{3} \sqrt{\frac{\delta}{2}} (\delta - s) \delta \eta_1, \quad (100.0)$$

$$I_{0,-1,3}^1 = \frac{8}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{3}{10} g_3 + \frac{1}{4} (2\delta - s)g_2 + \frac{4}{3} h(\delta - s)^2 \right\} \delta \omega_1 \\ - \frac{8}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{9}{20} g_2 + 4\delta(\delta - s) \right\} \delta \eta_1, \quad (100.1)$$

$$I_{0,-1,2}^2 = \frac{8}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{5}{112} g_2^2 + \frac{1}{5} (4\delta - s) g_3 + \frac{1}{12} (8\delta^2 - 4\delta s - s^2) g_2 + \frac{4}{3} h^2 (\delta - s)^2 \right\} \delta \omega_1 - \frac{8}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{7}{3} g_3 + \frac{3}{10} (4\delta - s) g_2 + \frac{4}{3} h (\delta - s) (4\delta - s) \right\} \delta \eta_1, \quad (100.2)$$

$$I_{0,-1,3}^2 = \frac{8}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{1}{10} g_2 g_3 + \frac{5}{336} (10\delta - s) g_2^2 + \frac{1}{30} (40\delta^2 - 8\delta s - 5s^2) g_3 + \frac{1}{36} h (40\delta^2 - 32\delta s + s^2) g_2 + \frac{4}{3} (\delta - s)^2 h^3 \right\} \delta \omega_1 - \frac{8}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{7}{80} g_2^2 + \frac{1}{7} (10\delta - s) g_3 + \frac{1}{20} (40\delta^2 - 8\delta s - 5s^2) g_2 + \frac{4}{3} h^2 (\delta - s) (5\delta - 2s) \right\} \delta \eta_1. \quad (100.3)$$

If, finally, $\gamma = 5$,

$$I_{0,-1,5}^0 = -\frac{16}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{3}{10} g_3 + \frac{1}{2} (\delta - s) g_2 + \frac{8}{9} (\delta - s)^2 \right\} \delta^2 \omega_1 + \frac{16}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{9}{20} g_2 + 4(\delta - s)^2 \right\} \delta^2 \eta_1, \quad (101.0)$$

$$I_{0,-1,5}^1 = -\frac{16}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{5}{112} g_2^2 + \frac{1}{10} (8\delta - 5s) g_3 + \frac{1}{6} (\delta - s) (4\delta - s) g_2 + \frac{8}{9} h (\delta - s)^2 \right\} \delta^2 \omega_1 + \frac{16}{3} \sqrt{\frac{\delta}{2}} \left\{ \frac{3}{7} g_3 + \frac{3}{20} (8\delta - 5s) g_2 + \frac{4}{9} (\delta - s)^2 (8\delta + s) \right\} \delta^2 \eta_1. \quad (101.1)$$

The two remaining rotational terms are of the form (46.1) and become

$$I_{0,1,1}^0 = \sqrt{\frac{\delta}{2}} \left\{ \frac{2}{5} g_2 \eta_1 - \frac{3}{5} g_3 \omega_1 \right\}, \quad (102.0)$$

$$I_{0,1,1}^1 = \sqrt{\frac{\delta}{2}} \left\{ \frac{3}{7} g_3 + \frac{2}{5} h g_2 \right\} \eta_1 - \sqrt{\frac{\delta}{2}} \left\{ \frac{1}{42} g_2^2 + \frac{3}{5} h g_3 \right\} \omega_1. \quad (102.1)$$

Equations (99)–(102) are valid irrespective of whether the eclipse is partial or annular.

21. The remaining part f_2 of the boundary corrections, due to the distortion of the eclipsing component, can be expressed in terms of integrals of the form $I_{\alpha,\beta,\gamma}^m$ as defined by equation (72). These integrals are evidently of the same form as the previously treated $I_{\alpha,\beta,\gamma}^m$'s, and the methods of solution investigated in section IV are therefore applicable. Equations (71.0) and (71.1) show that, to the order of accuracy we are working, terms associated with tidal distortion are of the form $I_{-1,0}^m$ if the eclipsed star is uniformly bright, and $I_{-1,1}^m$ in the case of complete darkening. The former terms are all elementary and can be dealt with in terms of circular and algebraic functions; the latter are found to involve elliptic integrals.

As to terms of the former kind we easily establish by direct integration that, if the eclipse is partial,

$$\pi I_{-1,0}^0 = \cos^{-1} \xi, \quad (103.0)$$

$$\pi I_{-1,0}^1 = \sqrt{1 - \xi^2}, \quad (103.1)$$

where

$$\xi = \frac{\delta - s}{r_2},$$

and with the aid of the recursion formula

$$\pi m I_{-1,0}^m = \pi(m-1) I_{-1,0}^{m-2} + \xi^{m-1} \sqrt{1-\xi^2}, \quad (104)$$

it follows that

$$I_{-1,0}^2 = \frac{1}{2\pi} \{ \cos^{-1} \xi + \xi \sqrt{1-\xi^2} \}, \quad (103.2)$$

$$I_{-1,0}^3 = \frac{1}{3\pi} \{ \xi^2 + 2 \sqrt{1-\xi^2} \}, \quad (103.3)$$

$$I_{-1,0}^4 = \frac{1}{8\pi} \{ 3 \cos^{-1} \xi + \xi(2\xi^2 + 3) \sqrt{1-\xi^2} \}. \quad (103.4)$$

During annular phase these expressions reduce to

$$I_{-1,0}^{2\mu} = \left(\begin{matrix} \mu - \frac{1}{2} \\ \mu \end{matrix} \right) \quad \text{and} \quad I_{-1,0}^{2\mu+1} = 0, \quad (105)$$

as to whether their superscript is even or odd.

In the case of complete darkening at limb the integrals associated with tidal distortion are of the form $I_{-1,1}^m$ which take the explicit forms

$$\pi r_2 I_{-1,1}^0 = 2\sqrt{2\delta} \{ \eta_1 + e_2 \omega_1 \}, \quad (106.0)$$

$$\pi r_2^2 I_{-1,1}^1 = \sqrt{2\delta} \left\{ e_2 \eta_1 + \left(\frac{1}{6} g_2 - e_2^2 \right) \omega_1 \right\}, \quad (106.1)$$

$$\pi r_2^3 I_{-1,1}^2 = \frac{1}{10} \sqrt{2\delta} \{ 3g_2 - 15e_2^2 \} \eta_1 - \frac{1}{10} \sqrt{2\delta} \{ 2g_3 - 5e_2^3 \} \omega_1, \quad (106.2)$$

$$\pi r_2^4 I_{-1,1}^3 = \frac{1}{20} \sqrt{2\delta} \left\{ 13e_2^3 - \frac{19}{7} g_3 \right\} \eta_1 + \frac{1}{20} \sqrt{2\delta} \left\{ \frac{25}{42} g_2^2 + \frac{9}{2} e_2 g_3 - 15e_2^4 \right\} \omega_1, \quad (106.3)$$

$$\begin{aligned} \pi r_2^5 I_{-1,1}^4 = \frac{1}{120} \sqrt{2\delta} \left\{ 7g_2^2 + \frac{366}{7} e_2 g_3 - 177e_2^4 \right\} \eta_1 \\ - \frac{1}{120} \sqrt{2\delta} \left\{ 8g_2 g_3 + \frac{25}{7} e_2 g_2^2 + 8e_2^2 g_3 - 95e_2^5 \right\} \omega_1. \end{aligned} \quad (106.4)$$

These equations are again valid irrespective of whether the eclipse is partial or annular. The $I_{-1,1}^m$'s can easily be rewritten in terms of complete elliptic integrals of the first and second kind; doing so we obtain

$$I_{-1,1}^0 = \frac{2}{\pi} \sqrt{\frac{\delta}{r_2}} \{ 2E - (1 + \xi)F \}, \quad (106.01)$$

$$I_{-1,1}^1 = \frac{2}{3\pi} \sqrt{\frac{\delta}{r_2}} \{ (1 + \xi)F - 2\xi E \}, \quad (106.11)$$

$$I_{-1,1}^2 = \frac{2}{15\pi} \sqrt{\frac{\delta}{r_2}} \{ 2(9 - 2\xi^2)E - (1 + \xi)(9 - 2\xi)F \}, \quad (106.21)$$

$$I_{-1,1}^3 = \frac{2}{105\pi} \sqrt{\frac{\delta}{r_2}} \{ (1 + \xi)(25 - 6\xi + 8\xi^2)F - \frac{4}{105\pi} \sqrt{\frac{\delta}{r_2}} \{ 19\xi + 8\xi^3 \} E, \quad (106.31)$$

$$\begin{aligned} I_{-1,1}^4 = \frac{4}{315\pi} \sqrt{\frac{\delta}{r_2}} \{ 147 - 24\xi^2 - 16\xi^4 \} E \\ - \frac{2}{315\pi} \sqrt{\frac{\delta}{r_2}} \{ (1 + \xi)(147 - 36\xi + 12\xi^2 - 16\xi^3) \} F, \end{aligned} \quad (106.41)$$

if the eclipse is partial, and

$$I_{-1,1}^0 = \frac{4}{\pi\kappa} \sqrt{\frac{\delta}{r_2}} E, \quad (106.02)$$

$$I_{-1,1}^1 = \frac{4}{3\pi\kappa} \sqrt{\frac{\delta}{r_2}} \{(1 + \xi)F - \xi E\}, \quad (106.12)$$

$$I_{-1,1}^2 = \frac{4}{15\pi\kappa} \sqrt{\frac{\delta}{r_2}} \{(9 - 2\xi^2)E + 2\xi(1 + \xi)F\}, \quad (106.22)$$

$$I_{-1,1}^3 = \frac{4}{105\pi\kappa} \sqrt{\frac{\delta}{r_2}} \{(1 + \xi)(25 + 8\xi^2)F - \xi(19 + 8\xi^2)E\}, \quad (106.32)$$

$$I_{-1,1}^4 = \frac{4}{315\pi\kappa} \sqrt{\frac{\delta}{r_2}} \{(147 - 24\xi^2 - 16\xi^4)E + 4\xi(1 + \xi)(9 + 4\xi^2)F\}, \quad (106.42)$$

if it is annular.

The rotational distortion of the eclipsing component invokes, in addition to terms already treated, new terms of the form $I_{1,0}^0$, if the eclipsed star is uniformly bright, and $I_{1,1}^0$ in the case of complete darkening. The former integral is an elementary one; for we obtain at once that

$$I_{1,0}^0 = I_{-1,0}^0 - I_{-1,0}^2. \quad (107)$$

$I_{1,1}^0$ is an elliptic integral, the evaluation of which yields

$$\pi r_2^3 I_{1,1}^0 = \frac{1}{5} \sqrt{\frac{\delta}{2}} \{2g_2\eta_1 - 3g_3\omega_1\} \quad (108.0)$$

or, in terms of Legendre normal forms,

$$I_{1,1}^0 = \frac{4}{15\pi} \sqrt{\frac{\delta}{r_2}} \{2(3 + \xi^2)E - (1 + \xi)(3 + \xi)F\} \quad (108.10)$$

if the eclipse is partial, and

$$I_{1,1}^0 = \frac{8}{15\pi\kappa} \sqrt{\frac{\delta}{r_2^2}} \{(3 + \xi^2)E - \xi(1 + \xi)F\} \quad (108.11)$$

if it is annular.

22. An inspection of equations of preceding paragraphs shows that the functions $\mathfrak{Z}_{\beta,\gamma}^m$ as well as $I_{\beta,\gamma}^m$ turn out to be also dimensionless quantities which can be made to depend upon two independent variables—say k and p —and tabulated in terms of such parameters similarly as the associated α -functions. Concerning the particular values which these functions may assume, it is evident that all boundary corrections should vanish at the moment of the first contact and—if $r_1 < r_2$ —also at the beginning of the totality. In this latter case we thus again have

$$\mathfrak{Z}_{\beta,\gamma}^m(k, \pm 1) = I_{\beta,\gamma}^m(k, \pm 1) = 0 \quad (109)$$

for any value of the subscripts and of m . If, however, $r_1 > r_2$, the boundary corrections do not vanish and remain finite²⁶ at the moment of internal tangency. Finally, at the moment of central eclipse

²⁶ If $r_1 > r_2$, the modulus of elliptical integrals in expressions with β and γ odd approaches unity at the moment of internal tangency, and hence $F\left(\frac{\pi}{2}, \kappa\right) \rightarrow \infty$. Since, however (cf. Whittaker and Watson, *op. cit.*, sec. 22.737),

$$\lim_{\kappa \rightarrow 1} \left\{ F\left(\frac{\pi}{2}, \kappa\right) - \log \frac{4}{\sqrt{1 - \kappa^2}} \right\} = 0,$$

it follows that

$$\lim_{\kappa \rightarrow 1} (1 + \xi) F\left(\frac{\pi}{2}, \kappa\right) = \lim_{\kappa \rightarrow 1} 2(1 - \kappa^2) F\left(\frac{\pi}{2}, \kappa\right) = 0$$

and the singularity is therefore only an apparent one.

($\delta = 0$), the only boundary corrections with non-vanishing coefficients are again those of zero order which reduce to

$$\pi \mathfrak{Z}_{\beta, \gamma}^0(k, -1/k) = B(\frac{1}{2}, \frac{1}{2}\beta + 1)k^{\beta+2}(1 - k^2)^{\gamma/2} \quad (110)$$

and

$$\pi I_{\beta, \gamma}^0(k, -1/k) = B(\frac{1}{2}, \frac{1}{2}\beta + 1)k^{-\gamma}(1 - k^2)^{\gamma/2}. \quad (111)$$

Numerically, both the $\mathfrak{Z}_{\beta, \gamma}^m$'s and $I_{\beta, \gamma}^m$'s diminish with increasing subscripts, and very rapidly with increasing superscript—much more rapidly than the respective associated α -functions. None of the terms entering in equations defining the theoretical light curves requires any additional integrations and hence the solution of our problem is complete.

VII. DISCUSSION

23. In preceding sections formulae were set up which express the changes of light exhibited by close binary systems between minima as well as during eclipses, taking account of effects invoked by the second, third, and fourth spherical harmonic deformations. The results we found are by no means simple, and are likely to remain of little practical use unless the associated α -functions as well as functions expressing the boundary corrections are available in tabular forms. But once this has been done, theoretical light curves can be computed rigorously from a given set of parameters and compared with observations with minimum of difficulty.

The primary task which a computer of orbits of eclipsing binaries has to cope with is therefore the derivation of parameters specifying a light curve. In case of systems with well-separated components these can be obtained by a straightforward application of elementary methods to an observed light curve as it stands. If, however, the components get closer and the continuous changes of light between minima (due to the ellipticity and reflection effects) become too conspicuous to be neglected, Russell²⁷ proposed to "rectify" a light curve before analyzing it for orbital elements—that is, to apply empirically to the whole light curve certain harmonic terms required to render the light between minima constant. It is then assumed that such a rectified curve is equivalent to one that would be produced by the eclipse of two spherical stars, and to which the elementary methods of solution can be applied.

Let us investigate, in the light of the preceding results, the extent to which this assumption can hold true. If we generalize equations (88) for any value of p between ± 1 by putting

$$\alpha_{2\nu}^{2\mu}(k, p) = \frac{\nu! \Gamma(\mu + \frac{1}{2})}{\sqrt{\pi}(\mu + \nu + 1)!} \alpha_0^0(k, p) + A_{2\nu}^{2\mu}(k, p), \quad (112.0)$$

and

$$\alpha_{2\nu-1}^{2\mu}(k, p) = \frac{3\Gamma(\mu + \frac{1}{2})\Gamma(\nu + \frac{1}{2})}{2\sqrt{\pi}\Gamma(\mu + \nu + \frac{3}{2})} \alpha_1^0(k, p) + A_{2\nu-1}^{2\mu}(k, p), \quad (112.1)$$

then, to the second-order harmonic distortion, the "uniform" loss of light at any moment during eclipse assumes the form

$$\begin{aligned} \Delta \mathcal{Q}^U = \{ & 1 + [2 + \frac{1}{2}\Omega_2^U][\frac{1}{2}v_1^{(2)}P_2(n_0) - w_1^{(2)}P_2(l_0)] \} \{ \alpha_0^0 + [v_1^{(2)}n_0n_2 \\ & - 3w_1^{(2)}l_0l_2][\alpha_1^0 + \Omega_2^U\alpha_1^1] + \frac{1}{2}\Omega_2^U[v_1^{(2)}(n_0^2 - n_1^2) - 3w_1^{(2)}l_0^2]A_2^0 \\ & + \frac{1}{2}\Omega_2^U[v_1^{(2)}(n_2^2 - n_1^2) - 3w_1^{(2)}l_2^2]A_0^2 + \text{boundary corrections} \}; \end{aligned} \quad (113.0)$$

while if the eclipsed star is completely darkened at limb,

$$\begin{aligned} \Delta \mathcal{Q}^D = \frac{3}{2} \{ & 1 + \frac{1}{2}[5 + \frac{1}{2}\Omega_2^D][\frac{1}{2}v_1^{(2)}P_2(n_0) - w_1^{(2)}P_2(l_0)] \} \{ \alpha_1^0 + [v_1^{(2)}n_0n_2 \\ & - 3w_1^{(2)}l_0l_2][2\alpha_0^1 + \Omega_2^D\alpha_1^1] + \frac{1}{2}\Omega_2^D[v_1^{(2)}(n_0^2 - n_1^2) - 3w_1^{(2)}l_0^2]A_3^0 \\ & + \frac{1}{2}\Omega_2^D[v_1^{(2)}(n_2^2 - n_1^2) - 3w_1^{(2)}l_2^2]A_1^2 + \text{boundary corrections} \}. \end{aligned} \quad (113.1)$$

Contributions to the light changes arising from the third and fourth harmonic tidal distortions can be rewritten similarly.

²⁷ *Ap.J.*, 36, 54, 1912.

If we compare equation (113.0) or (113.1) with (73), we notice that in either case terms in the first curly brackets on the right-hand sides of (113.0) or (113.1) are identical with those invoking the variation of light between eclipses and can presumably be removed by rectification. The remaining terms, in second curly brackets, then represent the rectified theoretical light curve within minima. This, in addition to the fundamental modes α_0^0 or α_1^0 , contains a number of terms of the first order which—however small—are of the same order of magnitude as those responsible for the variation of light between minima. The rectification therefore removes only a part of terms arising from the distortion. It can render a light curve simpler, but can by no means free it from all effects of distortion. Thus the vital assumption underlying the process of rectification—namely that a rectified light curve corresponds to one produced by the eclipse of two spherical stars—is not fulfilled to a higher approximation.

24. In view of the applications, it is desirable to pick up from (113) terms which are likely to be most important in practical cases. As the reader may easily visualize, an essential condition for the occurrence of eclipses is that the direction cosines l_2 and n_0 are of the same order of magnitude as the fractional radii of both components. Hence, as far as effects of the order of second harmonic distortions are concerned, quantities of the order of $l_2 w^{(2)}$ or $n_0 w^{(2)}$ are clearly negligible. The matters can be further simplified somewhat if we modify our definition of standard radius of a distorted star. So far (cf. sec. II) the standard radius has been defined as one of a sphere equal in volume to the distorted ellipsoid. This quantity does not, however, follow directly from preliminary orbital solution. The conventional "radii" of the components resulting from such a solution are very approximately equal to the diametral semi-axes of the actual ellipsoids.²⁸ If $a > b > c$ are the fractional semi-axes of an ellipsoidal star, then r , radius of a sphere of equal volume, is evidently $\sqrt[3]{abc}$; while the diametral semi-axis b , to the second-order harmonic distortion, becomes

$$b = r(1 - \frac{1}{6}v^{(2)} + \frac{1}{2}w^{(2)} + \dots). \quad (114)$$

Let us eliminate by means of this equation r from (19) and subsequent equations, and adopt b as the standard radius of a distorted star. If we now abbreviate

$$\bar{v}_{1,2}^{(2)} = \left(1 + \frac{m_{2,1}}{m_{1,2}}\right) \Delta_2 b_{1,2}^3, \quad \bar{w}_{1,2}^{(j)} = \frac{m_{2,1}}{m_{1,2}} \Delta_j b_{1,2}^{j+1}, \quad j = 2, 3, 4, \quad (10.1)$$

where the subscripts 1, 2 will refer to the primary (eclipsed) and secondary (eclipsing) component respectively, and make use of the algebraic identities

$$\begin{aligned} 3\bar{v}_{1,0}^0 + 2A_2^0 + 2A_0^2 &= (r_2/r_1)^2 I_{1,0}^0, \\ 3\bar{v}_{-1,2}^0 - 2A_2^0 &= 0, \end{aligned}$$

then by combining the boundary corrections due to the distortion of both components we find that the "uniform" rectified theoretical light curve reduces to

$$\Delta \mathcal{Q}_{\text{rec}}^U = \alpha_0^0 + \{\bar{v}_1^{(2)} - \bar{v}_2^{(2)}\} (r_2/r_1)^2 I_{1,0}^0 - \{2 + \frac{1}{2}\Omega_2^U\} \{\bar{v}_1^{(2)}[A_2^0 + A_0^2] + 3\bar{w}_1^{(2)}A_2^0\} + \dots \quad (115)$$

To this order of accuracy the rectified light curve does not involve the direction cosines l or n , and the light changes are therefore independent of the scale of each particular system.

Of the two first-order terms on the right-hand side of (115), the term

$$\{\bar{v}_1^{(2)} - \bar{v}_2^{(2)}\} (r_2/r_1)^2 I_{1,0}^0 \quad (116)$$

is purely geometrical and accounts for the difference in polar flattening of both components; while

$$\{2 + \frac{1}{2}\Omega_2^U\} \{\bar{v}_1^{(2)}[A_2^0 + A_0^2] + 3\bar{w}_1^{(2)}A_2^0\} \quad (117)$$

arises in connection with gravity-darkening. The former term consists of a difference of small quantities, and unless both components are very unequal in form it is likely to be minor. The latter consists, however, of a sum of small quantities and is therefore likely to be the dominant one. To this order of accuracy, the rectified light curve does not depend upon the tidal distortion of the

²⁸ I.e., to the radii of their diametral cross-sections which are circles for tidally distorted stars.

secondary component.²⁹ This is easy to understand; for the tides do not affect the diametral cross-section (exposed to us within minima) of the distorted stars. Tidal distortion of the eclipsed star enters into (115) only indirectly, through the gravity-darkening.

Were the gravity effect non-existent, it would follow from equation (68) that $\Omega_2^U = -4$, in which case (117) vanishes; and so does (116) if $\bar{v}_1 = \bar{v}_2$. Thus, for uniformly bright stars, the process of rectification would apply rigorously if both components were prolate spheroids or similar three-axial ellipsoids. These facts have already been pointed out by Russell.²⁷ On the other hand, if we take the coefficient of gravity-darkening appropriate for integrated radiation, $\Omega_2^U = 0$, and equations (113) or (115) also undergo considerable reduction. There is, however, no special likelihood that Ω_2^U should vanish, and it is physically impossible that it could reach -4 . In practical cases Ω_2^U will generally be neither zero nor an integer, and may be positive or negative. Equation (115) is then to be used as it stands.

In the case of limb-darkening, equation (113.1) admits of an analogous simplification, but the functions associated with the distortion are considerably more complicated. Fortunately, it does not appear necessary to investigate them at present to the same detail. For equation (17.0) can evidently be rewritten as

$$\Delta Q = \Delta Q^U + \frac{2u}{3-u} (\Delta Q^D - \Delta Q^U). \quad (17.1)$$

The "darkened" functions are therefore found to enter, not in their absolute values, but only through differences between the corresponding "uniform" and "darkened" functions. If the coefficient of darkening is small, then within the scheme of our approximation we may neglect the differences of small quantities and retain only the zero-order term

$$\frac{2u}{3-u} (\alpha^D - \alpha^U);$$

but if the darkening is complete or nearly so, the differences of small quantities may become noticeable and should be considered.³⁰

25. Equations (113) or (115) hold good no matter whether the eclipse is partial or annular. In the latter case, however, (115) admits of considerable simplification. For in section VI we found that, during annular phase, $\alpha_0^0 = k^2$, $I_{-1,0}^0 = \frac{1}{2}$, and

$$A_0^2 = +k^2 \{ D^2 - \frac{1}{4}(1 - k^2) \}, \quad (118.0)$$

$$A_2^0 = -k^2 \{ D^2 - \frac{1}{2}(1 - k^2) \}. \quad (118.1)$$

²⁹ As was already discussed by the writer in *Ap.J.*, **94**, 159, 1941 (sec. IV), the effect of tidal distortion of the eclipsing component, small as it is, tends to simulate increased limb darkening of the eclipsed star. The proof as given in section IV of that paper is, unfortunately, obscured by the fact that radius of a sphere of equal volume as the distorted ellipsoid was used as the standard radius of the secondary component. If, as above, the diametral semi-axis is adopted as standard radius instead, the radial-expansion terms $I_{-1,0}^0$ or $I_{-1,1}^0$ disappear from equations (9) or (10) of the paper referred to, while equation (9.1) of the same paper should be replaced by

$$k^2 f_2^U \doteq 3\bar{w}_2^{(2)} \bar{g}^2 I_{-1,0}^2 - \bar{v}_2^{(2)} I_{1,0}^0.$$

Neglecting differences of small quantities, the loss of light due to the eclipse of a spherical star becomes

$$\Delta Q = \alpha^U + f_2^U + \frac{2u}{3-u} (\alpha^D - \alpha^U).$$

Near the inner contact and in advanced partial stages $I_{-1,0}^2$ and $I_{1,0}^0$ are positive and increasing functions of the geometrical depth; but so is the difference $\alpha^D - \alpha^U$. Hence the effect of the tidal term in equation (9.1) will evidently be to simulate increased limb darkening of the eclipsed star, while the rotational term will tend to do the opposite. These are the conclusions reached in the writer's previous paper. The validity of equivalence between distortion and darkening is, however, limited; and on the basis of more numerical computations it appears now dubious to the writer whether equations (28.0) and (28.2) of that paper or analogous relations can possess much practical meaning.

³⁰ Provided, of course, that the degree of limb-darkening is sufficiently well known; for otherwise the uncertainty of the zero-order term, caused by our incomplete knowledge of darkening, may introduce errors comparable with those arising from the neglect of differences of small quantities.

Hence $A_0^2 + A_2^2 = \frac{1}{4}k^2(1 - k^2)$, and the rectified uniform loss of light then takes the form

$$\Delta \mathcal{L}^U = \alpha_0^0 \left\{ 1 + \frac{1}{2} [\bar{v}_1^{(2)} - \bar{v}_2^{(2)}] - \frac{1}{2} (1 - k^2) (1 + \frac{1}{4} \Omega_2^U) [\bar{v}_1^{(2)} + 6\bar{w}_1^{(2)}] + \frac{3}{2} (1 + \frac{1}{4} \Omega_2^U) \bar{w}_1^{(2)} D^2 + \dots \right\}. \quad (119)$$

Of the two terms in curly brackets on the right-hand side of equation (115) the first one, arising from the difference in polar flattenings of both components, becomes constant during annular phase, and so does the second term in so far as it depends on flattening of the eclipsed star. Thus, to the order of accuracy we are working, the only term varying with the geometrical depth is

$$+ \frac{3}{2} (1 + \frac{1}{4} \Omega_2^U) \bar{w}_1^{(2)} D^2, \quad (120)$$

and arises from the gravity-darkening due to the tidal distortion of the eclipsed primary star. In the absence of ordinary limb-darkening the rectified loss of light should therefore reach its maximum at the moment of internal tangency, and decrease henceforth continuously with diminishing geometrical depth of the eclipse; a rectified light curve should be convex upwards during annular phases. This is easy to understand; for the distribution of brightness on the surface of a tidally distorted star, due to the gravity effect and viewed from the direction of its longest axis, is tantamount to limb-brightening.²¹ If, however, the limb- and gravity-darkenings superpose, the situation becomes too complex to be analyzed in simple terms; and the increase of brightness from center to limb needs no longer to take place. The rectified light during annular phases may then remain sensibly constant, or may actually decrease with decreasing geometrical depth, as it would do if the eclipsed star were darkened at limb but the gravity-darkening were absent.

26. The application of the preceding results to practical cases can best proceed by the "method of false position."²² After having performed an empirical rectification we neglect, at first, the remaining effects of distortion and solve our light curve by elementary methods. With the aid of rough elements thus obtained we compute the true theoretical light curve, including the effects of distortion, and compare with observations. The simplified forms (115) or (119) can preferably be used for the second approximation. Let O be the observed curve, and C the computed one. Construct now a new curve which is at every point as far below O as C is above it. From this curve, by the same method of solution, derive new elements and from these a new computed curve C' . The latter should be much closer to O than C was. Repetition of this process, if necessary, should result in a good fit. There is no general guarantee that such approximations will converge in every practical case; yet if they fail, there is but little hope that the far more laborious adjustment by least squares would improve the results. Only after a really good fit has thus been obtained is it justifiable to attempt the latter—remembering that the test of a good preliminary job is that the least-squares corrections should be of the same order of magnitude as their probable errors.

The procedure described above is not likely to be unduly laborious, but is admittedly much more involved than the simple form of solution applicable if the effects of distortion are neglected. As long as both components can be regarded as circular disks with uniform or radially symmetrical distribution of brightness the orbital problem is simple; and to this extent it was exhaustively dealt with in the classical memoirs by Russell and Shapley²³ thirty years ago. At that time the photo-electric photometry was still in its infancy; and errors of normal magnitudes constituting the best light curves then available were as a rule measured in hundredths of a magnitude. In the three decades which elapsed since that time, however, the accuracy of photometric measurements has been increased about ten times; and precise light curves of several close binaries, produced in recent years, have exceeded very definitely our ability of interpreting them; the simplified model underlying Russell's method proved no longer adequate.

The aim of the present paper has been to start from a model corresponding more closely to reality, and to extend the background of our interpretation of light curves as far as it proves practicable at

²¹ Cf. Russell, *Ap.J.*, 90, 641, 1939 (p. 660).

²² The writer owes this suggestion to Professor Russell. (Cf. a forthcoming paper by Professor Russell in the *Astrophysical Journal*.)

²³ Russell, *Ap.J.*, 35, 315, and 36, 54, 1912; Russell and Shapley, *Ap.J.*, 36, 239, 385, 1912.

the present state of research. And it is believed that, unless a system is so close that its components are nearly in contact, our results should enable one to carry out an analysis of light curves, based on a physically sound and consistent model, up to quantities of the order of one or two thousandths of a magnitude. The situation arising thus in orbital analysis of eclipsing binaries may be compared with that experienced in the early days of celestial mechanics, when the Keplerian ellipses—an analogon to the simplified form of problem treated by Russell and Shapley—proved inadequate to represent the orbits of bodies in our solar system with sufficient accuracy, and recourse had ultimately to be made to the theory of general perturbations.

In conclusion, the writer takes pleasure in expressing his appreciation to Professor Henry Norris Russell for stimulating interest, and to Dr. Harlow Shapley for constant generous encouragement to which the present paper owes a great deal.



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